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Project Completion
Report No.
710799-760851

PRODUCTIVITY OF GREAT LAKES ZOOPLANKTON

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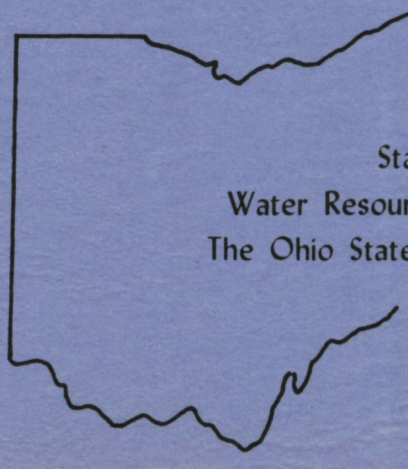
May 1980

United States
Department of the Interior

Contract No.
A- 048 -Ohio



State of Ohio
Water Resources Center
The Ohio State University

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15 May 1980

This study was supported in part by the Office of Water Resources Technology, U. S. Department of Interior under project A-048-OHIO

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ABSTRACT

A mathematical model of zooplankton productivity for the Laurentian Great Lakes has enabled us to calculate productivity rates for Cladocera, Copepoda, and Rotifera from Lakes Ontario and Erie. Productivity values from the Bay of Quinte, Lake Ontario, demonstrated that nearshore productivity and biomass varied greatly along with algal abundance and temperature. Increasing the loading of phosphorus and nitrogen did not directly result in higher zooplankton and phytoplankton productivity in this eutrophic arm of Lake Ontario. A study of 30 stations in Lake Erie on 10 monthly cruises showed that total productivity of the zooplankton community is strongly correlated with temperature, but that individual taxa varied significantly throughout the season. Productivity in the open water of Lake Erie (1970) was much less than the values observed in the Lake Erie and Lake Ontario nearshore zones. We are currently preparing a data set from the Western Basin of Lake Erie for the 1948-49 field year which will allow us to calculate productivity of zooplankton from that year for comparison with current patterns.

Comparison of the roles of Copepoda, Cladocera, and Rotifera in the over-all productivity showed that Copepoda predominated in the spring, along with rotifers, but that Cladocera were the most important producers during the summer.

Measurements of cladoceran size at first reproduction showed that they reach maturity at a large size in the spring and decline in size at maturity through the summer, with all species declining in size in a synchronous pattern. It is suggested that this pattern results from the combined effects of size-selective predation by fish and competition among cladocerans for food. Similar patterns were observed for copepods.

Key Words

Great Lakes, zooplankton, productivity, Cladocera, Copepoda, Rotifera, Lake Erie, Lake Ontario, toxicity, non-ionic detergents

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INTRODUCTION

Although primary productivity of lakes can be measured with reasonable accuracy, there is no similar technique that will measure the transfer of the fixed energy to the next trophic levels, including zooplankton and fish. In fact most impact studies and long term comparisons of zooplankton in Lake Erie depend upon simple comparisons of abundances of zooplankton in vertical net hauls, although it is known that the short generation time of zooplankton makes such comparisons uninformative. Cohort-based mortality studies which may be satisfactory with fish are not possible with zooplankton since survival and generation times are so short in zooplankton that one has essentially continuous recruitment.

Many zooplankton species occurring in the Great Lakes are quite seasonal in abundance; and all species go through marked oscillations in abundance, so comparisons based on numerical abundance often involve comparing a population size of 1000/liter on 23 June of one year with 0.01 per liter the next year on the same date. While single species do indeed vary this much, the overall biomass of organisms is not so variable, and the rate of production of that biomass varies over only one or two orders of magnitude for a given time of year from day to day or year to year.

Not only do the organisms vary in abundance seasonally, but the rate at which they mature, the duration of egg development, and growth rates are strongly affected by temperature. Hall (1964) showed that Daphnia galeata mendotae egg development time was strongly affected by temperature but that food had little effect on it, unless there was essentially none present. Accordingly, differences in abundance of zooplankters means one thing in the spring, while quite another in the summer when generation times can be eight times shorter.

The solution to the problem is to estimate the productivity of the population through a consideration of the biomass of each state of each species currently and the amount that species can be expected to grow during the next day at the given temperature at which it was collected. These individual estimates are then summed for the species present in the system to get the community productivity. The community estimate can be more easily compared with primary productivity estimates obtained from ^{14}C or oxygen light bottle-dark bottle techniques.

In this study, we have prepared a FORTRAN program which calculates the secondary productivity of zooplankton from the Laurentian Great Lakes, including the Cladocera, Rotifera, and Copepoda. A total of 140 species are included, although good estimates of biomass versus length relationships and development times are available for the species in Lakes Erie and Ontario only. It takes into account the variation in egg development and adult maturation times with temperature, and the variation of weight of an individual with increasing length. We have determined the latter for the major crustacean species of Lakes Erie and Ontario, and have extracted the development times from the literature. The accurate representation of the size distribution of organisms requires length-frequency measurements on the crustaceans, particularly the Cladocera, whose adult growth is indeterminate. The program merges the information on size-frequency with that on abundance to calculate productivity for each developmental stage and for egg production of each species.

The program has been used to calculate productivity in a series of fertilized enclosures in the Bay of Quinte, Lake Ontario, as compared with control enclosures and the open waters of the bay. We also compared the changes in productivity associated with the addition of a known amount of non-ionic detergent to two of the enclosures. The program has been used

to calculate productivity from a series of 10 cruises to 30 stations in Lake Erie made in 1970 by the Canada Centre for Inland Waters (CCIW). Rotifers were not enumerated in the original study by CCIW, so we have begun a study of them as well, and have completed the enumeration of the Western Basin samples. Productivity for the 1970 cruises will be compared with water quality parameters and primary productivity measurements made at the same stations and times as the plankton were collected. This will enable us to examine the influence of these variables on the productivity of the zooplankton.

The measurements of size frequency for cladocerans suggested a regular variation in the size at first reproduction for the Bay of Quinte samples in all species examined. Since this variation was unanticipated and had important implications for the interactions among fish predation, zooplankton competition, and the species composition of zooplankton communities, it was examined in greater detail, both for the Lake Ontario samples and in Lake Erie. For the latter, an examination of seasonal variation in adult sizes was also performed on the Copepoda.

In this report, I describe the details of the FORTRAN model, the biomass-length relationship measurements performed to use in it, our applications of the model to date, and our studies of the size at first reproduction of crustacean zooplankton of Lakes Erie and Ontario.

ZOOPR: A FORTRAN MODEL FOR CALCULATING THE PRODUCTIVITY OF GREAT LAKES ZOOPLANKTON

Program Rationale

ZOOPR was based on a model for production presented by Patalas (1970) who extended work done by Pechen and Shuskina (1964). The method is also described in Edmondson and Winberg (1971). Production per day is set equal to the number of organisms of a given species and instar (N_{ij}) multiplied by the increase in biomass resulting from growth to the next instar ($\Delta B_{ij \rightarrow j+1}$), divided by the time (in days) required to go from the current instar to the next ($T_{ij \rightarrow j+1}$). This productivity ($\mu g\ m^{-3}\ day^{-1}$) is summed for all instars and species. The model can thus be represented simply by:

$$P = \sum_{i} \sum_{j} \frac{N_{ij}\ \Delta B_{ij \rightarrow j+i}}{T_{ij \rightarrow j+i}}$$

where i refers to the species present, j refers to the specific instar under consideration and j+1 is the next instar. Egg production by adults can be included by setting ΔB_{ij} equal to the biomass of an egg. Obviously, no growth is associated with the hatching of an egg, and this term is thus in fact an estimate of adult reproductive output. If one assumes that the number of eggs in the population is constant over the 24 hr period, a new egg will be laid for each one hatched. Thus the number hatching (N_{ij}/T_{ij}) times the biomass of an egg (B_{ij}) gives the adult reproductive productivity, ignoring the production of sperm by males.

The three important taxonomic groups of zooplankton occurring in fresh water, the copepods, the cladocerans, and rotifers, have different development and growth patterns and thus are treated somewhat differently by the model; that is, the number of terms (j) required to represent the various stages

differs with each taxon. Rotifers have a very short post-hatching development time to the adult stage and grow little during this period, so they are treated by equating the total production of each species to the egg production.

Cladocerans brood their young, are parthenogenetic(primarily) like the rotifers, and therefore only females need be considered. There are three or four preadult instars but females continue to molt regularly for as long as they live. It is not possible to determine at what instar a cladoceran is merely by examining it. Instead we have established the minimum size at first reproduction (Culver 1980) from the size frequency distributions and set up six arbitrary, equal size classes between the neonate size (also determined from the size frequency distributions) and the size at first reproduction, and an additional seven classes between the size at first reproduction and the size of the ninty-five percentile for length. All larger individuals were put in an eighth size class (ninty-five percentile to hundred percentile) which was treated as terminal. Cladocerans thus either were eggs, one of six juvenile size classes or one of eight adult size classes. The individual length increments varied with the range of sizes of a given sample, a necessity generated by the seasonal variation in neonate and mature lengths. Determination of biomass associated with each size class and the development times ($T_{ij \rightarrow j+1}$) will be discussed in a subsequent section.

Copepods pass through six naupliar and five copepodite stages before reaching adulthood. Males and females are equally represented in most populations, and all reproduction is sexual. Ideally, the productivity equation would thus include one term for eggs (adult reproductive output), six naupliar terms, and five copepodite terms. Because it is extremely difficult to discern the species of naupliar stages beyond identification as calanoid or cyclopoid copepods, and because development times as a function of temperature for

individual stages are not generally known for naupliar or copepodite stages, we have formed the equation for copepods using either a single average naupliar biomass, early copepodite biomass and adult biomass, or we have used the above divided into arbitrary size ranges (six naupliar and five copepodite) using size-frequency information. In both cases, development times are based on the total time required to pass through the naupliar and copepodite phases respectively. In the latter case, we simply divide those numbers by six and five, respectively, to get the T_{ij}'s for the individual size classes. Sexual dimorphism is common in copepods, the female being the larger, so we estimated the ΔB for the sexually undifferentiated early copepodites by having them grow to male and female biomass in the same proportion as we observed adult males and females in the same sample. In the absence of definite data on the numbers of male and female adults (or the total absence of adults in the sample) we assumed half of the copepodites would grow to a male biomass and the other half would grow to a female biomass.

Structure of the program

While the complete listing of the program, flow chart and full description of the program is deferred to another publication (Culver and Osman 1980) due to length limitations, it is worthwhile to describe in brief how the program is structured.

There are basically two original data sets derived from the microscope work done on a field sample: the size frequency distribution and the abundance data. Because of their basic differences in data type, they are stored separately and then merged at a later step. Input formats vary according to the identification requirements dictated by the structure of the field sampling regime, but I have included that used for the Bay of Quinte which had seven sampling stations, four depths, and 25 dates (Appendix I) as an example.

Abundance values in this data set are recorded from the samples as females and eggs only for rotifers, as total adults, eggs, nauplii, copepodites, adult females, and adult males for copepods; and as eggs, ovigerous adults, or as non-ovigerous individuals for Cladocera.

Measurements for a given cladoceran species are sorted according to date (and by station if desired) and run through the proportional frequency program (PFREQ). The program sorts the measurements into ascending order by length and selects the tenth percentile for ovigerous females as the size at first reproduction. The fifth percentile for non-ovigerous individuals is selected as the neonate length, and the ninety-fifth percentile is taken from the ovigerous and non-ovigerous measurements together. This is repeated for each date and these lengths then used to generate the size increments for each date (i.e. juvenile size increment = one sixth of the difference between the neonate and the minimal adult length; adult size increments = one-seventh of difference between the ninety-fifth percentile and the minimal adult length). The neonate length, the size at first reproduction (SFR) and these two incremental values are then punched out on cards for each species and date, or written on a tape or disc file. This can then be used to adjust each set of productivity size classes according to the changing neonate and SFR lengths occurring in the field population.

Once the size classes for a given sampling date have been generated, it is then possible to go through the measurements on that date and construct a vector containing the proportion of individuals occurring in each size class. In the cladocerans for example, the relative proportions of individuals in each of the six juvenile size classes and each of the eight adult size classes are counted. Multiplying by the number per liter for each sample for that

date and station and depth generates a vector of abundances per liter, the N_{ij} values. The number of eggs per liter must be carried forward as well for the first $N_{i.}$.

Depths of the samples, or the depth of the water if a vertical tow was used are also extracted from the data cards to aid in calculating production per square meter. The other important datum to be fed into the computer is the temperature of the water from which the sample was taken. If the water is stratified thermally, it will be difficult to calculate development times particularly for vertical tow samples as will be seen below. We have integrated temperature curves to obtain average temperatures in such situations, but since the changes in development time with temperature are non-linear and the various species of zooplankton migrate vertically to varying amounts, this is at best a first approximation of the effective temperature at which the development of eggs or juveniles or, in the case of cladoceran adults, growth, will occur.

Determination of ΔB's

Once the neonate and SFR and size increments are known for a given sample and species, we obtain the ΔB_{ij}'s by calculating the biomass of an individual at the mid-point of each size class from regressions of dry weight as a function of length, either from Culver et al. (1980) or from the literature. The first juvenile size class of a cladoceran would be the neonate length plus one-half of the juvenile size increment for that species and date, with subsequent midpoints being one juvenile size increment further along until the SFR was reached. The process would then be repeated using adult size increments calculated as described above. The change in biomass associated in going from j to j+1 is simply the difference between the biomasses extracted from the regression equations. The values of B_{ij} are further

used by the program to calculate the biomass of each species in the sample in order to calculate the total zooplankton biomass for the productivity-biomass ratio (P/B) calculations.

Copepod biomass values were either constants, or were calculated as described above when measurements were available. All rotifer weights were entered into the program as constants.

Determination of Development Times ($T_{ij \rightarrow j+1}$)

Development times for rotifers are scarce in the literature, so we used a single equation based on egg development times from 15 species of rotifers, taken from Bottrell et al. (1976). Since we assume no growth from the egg stage to the adult, only egg development time is included (Appendix II).

Development times in the literature for copepods are primarily limited to egg development as a function of temperature (e.g. Cooley and Minns 1978), and development times through the naupliar and the copepodite stages are quite rare. We fitted polynomial equations to the data of Spindler (1971), Nauwerck (1963), and Hillbricht-Ilkowska and Patalas (1967) to obtain development time equations for these organisms. The species on which these equations were based were European, so this may be a significant source of error in our copepod productivity calculations.

Cladoceran developmental times are somewhat more tractable since the molting time of adults is exactly the same as the hatching time of the eggs. The function relating egg development time to temperature thus describes the time between adult molts as a function of temperature equally well. Unfortunately, we can not tell what instar a given cladoceran is by its length, so we cannot determine directly whether the size increment between two of our size classes is equivalent to that of one molt. If it is, then the time required

to go from one of our size classes to the next is equal to the time required for an egg to develop and hatch at that temperature. Because the temperature of the lakes varies seasonally and because we establish our size classes based on neonate size, size at first reproduction, and maximum observed size for a given sample, it is unlikely that one size class increment will be equal to one molting size increment very often. Accordingly, we have used a relationship described by Patalas (1970) to estimate what proportion of an egg development time to assign to the passing from one of our size increments to the next.

The method uses the observation that the length added to an individual during each adult molt is reasonably constant, and that the increment is about 1/3 the total increase in length between the cladoceran's neonate length and its length at maturity. Since we know the neonate and size at first reproduction lengths from our size-frequency measurements, we can calculate the increment added with each adult molt. By calculating what proportion of this increment is represented by one of our size increments, we know what proportion of one egg development time (at that temperature) is required for the species to go from one adult size class to the next. Juvenile development times were taken from the literature as the time from hatching to maturity, again as a function of temperature. Because the neonate and size at first reproduction lengths were known, juvenile size classes were defined as one sixth of this size increment, and we assigned one sixth of the total juvenile development time to each size increment. Juvenile development times for cladocerans are as rare as are naupliar development times for copepods, so this is again a source of error in our productivity estimates, because the same equations had to be used for cladocerans of various species.

We obtained cladoceran development time relationships from Bottrell (1975), Munro and White (1975), Hall (1964), and Hillbricht-Ilkowska and Patalas (1967) (Appendix II).

Determination of Specific Abundances (N_{ij})

As discussed above, the productivity calculation requires information on the abundance of individual size classes or instars.. The measurements of length-frequency are used to set up the categories of length for the productivity calculation as well as to determine the relative abundance of that species in each of those categories for length. For Cladocera, for example, we enumerate the individuals of each species in the sample and then measure a representative sample of individuals. The size-frequency data are then assigned to the categories generated from the neonate and SFR determinations. Once we have calculated the proportion of the measured individuals occurring in each of the 14 size categories (six juvenile and eight adult), we multiply this vector of proportions by the total abundance of that species in that sample to calculate the number of individuals per liter that belong in each of the size categories, that is the N_{ij}'s.

Calculation of productivity for that species then involves simply multiplying each N_{ij} by the $\Delta B_{ij \rightarrow j+1}$ that corresponds with it and dividing by the $T_{ij \rightarrow j+1}$ that also corresponds with it. These are then summed on j to get the total productivity of that species. Summing on i gives the total productivity for the sample. For the case of copepods, measurements are used to assign nauplii to six size classes, and copepodites are divided into five subadult categories, plus adult males and adult females, for a total of 13 size classes.

LENGTH-WEIGHT REGRESSIONS FOR ESTIMATION OF BIOMASS

One of the greatest needs for secondary productivity calculations identified at the beginning of this study was a series of accurate equations for estimating dry weight of Crustacea from the Great Lakes from length measurements. The indeterminate growth of Cladocera and the twelve developmental stages (and the sexual dimorphism of the adult stage) in Copepoda make the use of a single weight to represent a given species untenable. Accordingly, we determined the length-weight regressions for six copepod taxa and six cladocerans from Lake Erie. Two other Cladocera of interest, Chydorus sphaericus and Ceriodaphnia lacustris, were too rare in our Lake Erie samples, so we obtained organisms from samples taken in August 1974 in the Bay of Quinte, Lake Ontario (Table 1).

Zooplankters were anesthetized with carbonated water (Gannon and Gannon, 1975) and then preserved in four percent formalin or four percent formalin with 40 g/l sucrose added (Central Basin samples only) to prevent "ballooning" of cladoceran carapaces (Haney and Hall 1973).

Zooplankters were sorted by taxon, and each taxon was further sorted by length, sex and reproductive condition (females) with a dissecting microscope using magnifications of up to 200 diameters. Each plankter was measured with an ocular micrometer according to its body shape (Fig. 1). To minimize variance in the regressions, we selected individuals that were all exactly the same length ($\pm$ 10 μ) to the nearest ocular micrometer unit (1 unit = 20 μ at 100X) to constitute one sample. For the cyclomorphotic forms Daphnia retrocurva and D. galeata mendotae, we measured both from the anterior edge of the eye to the base of the tail spine (defined as standard length in this study) and from the anterior margin of the helmet to the base of the tail spine (defined as total length in this study). Because some investigators have

Table 1. Sampling sites for crustacean species included in the biomass study. (See Culver et al. 1980 for details)

TAXA	COLLECTION SITE NUMBER	COLLECTION DATE
Ceriodaphnia lacustris Birge	*	21 August 1974
Daphnia galeata mendotae Birge	2	28 July 1976
Daphnia retrocurva Forbes	3	28 July 1976
Bosmina longirostris(O. F. Müller)	4	30 August 1976
Eubosmina coregoni (Baird)	1	3 July 1976
Diaphanosoma leuchtenbergianum Fischer	4	30 August 1976
Chydorus sphaericus(O. F. Müller)	*	21 August 1974
Leptodora kindtii(Focke)	2	28 July 1976
Calanoid nauplii	1	6 August 1976
Diaptomus copepodites I-IV	1	6 August 1976
Diaptomus minutus Lilljeborg	1	3 July 1976
Diaptomus oregonensis Lilljeborg	1	1 August 1976
Diaptomus siciloides Lilljeborg	1	6 August 1976
Cyclopoid nauplii	1	6 August 1976
Cyclops bicuspidatus thomasi S. A. Forbes	4	30 August 1976
Cyclops vernalis Fischer	1	1 September 1976
Mesocyclops edax(S. A. Forbes)	4	30 August 1976

1 = Fishery Bay, South Bass Island, Western Lake Erie
2 = West of Bass Islands, Western Lake Erie
3 = Further West than Station #2
4 = Central Basin, Lake Erie
*Bay of Quinte, Lake Ontario

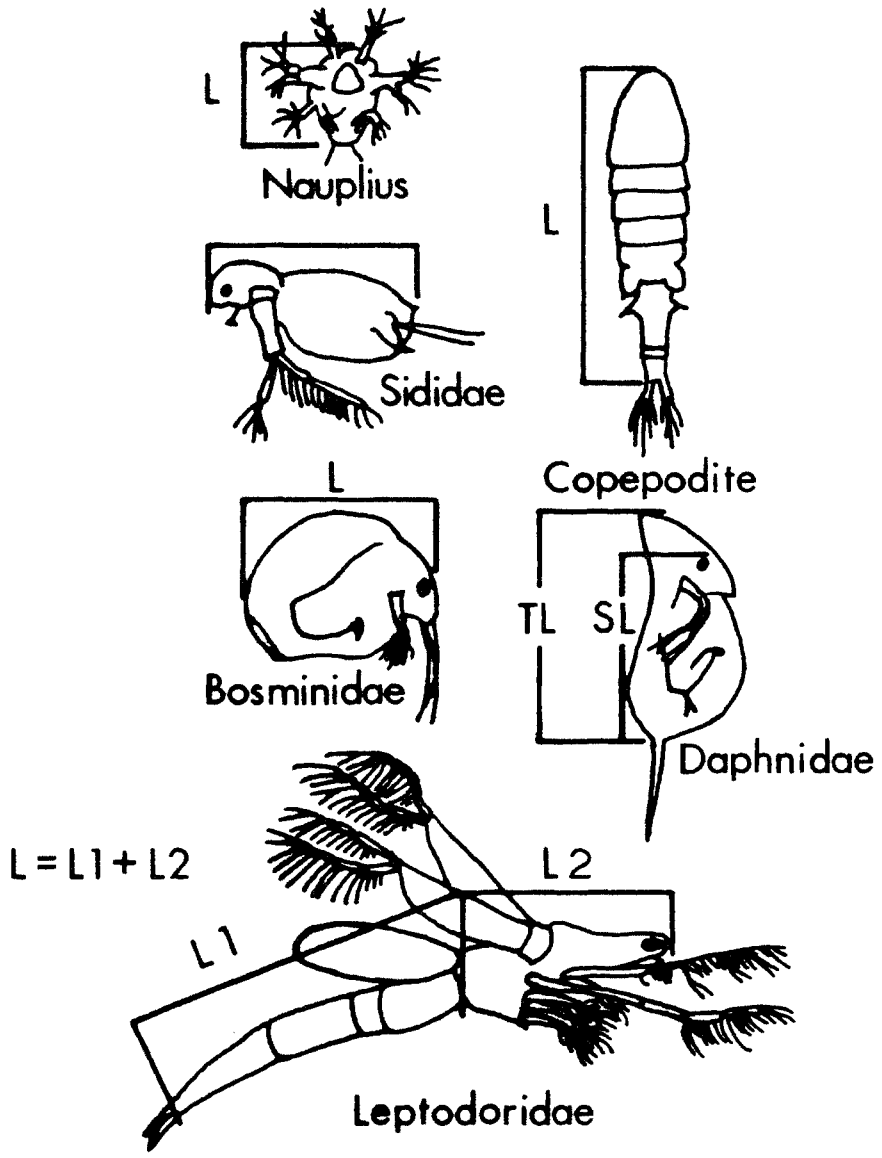

Figure 1. Method for measuring length for representative taxa. TL = total length, SL = standard length.

measured copepods to the base of the caudal spines, we have also done a study of the relative variation between this measure and our typical measure to the base of the caudal rami for Diaptomus minutus, D. oregonensis, D. siciloides, Cyclops vernalis, C. bicuspidatus thomasi, and Mesocyclops edax.

Sorted zooplankters were washed three times for thirty minutes in distilled water to remove the preservative and were transferred to a dried and tared platinum weighing pan with an Irwin loop (stainless steel wire with a 350 x 500 μm flattened loop). Weighing pans containing zooplankters were placed in a drying oven at 60°C for two hours. Drying was continued in a desiccator over calcium chloride for 24 hours before weighing the samples on a Cahn Gram electrobalance. For a given taxon, at least three samples for exactly the same length were weighed. The number of zooplankters used per weighing varied according to taxon and length, but sufficient organisms were added to achieve a minumum net weight of about 5 μg. This required 10-15 copepodites V, adult copepods, daphnids, or Leptodora kindtii individuals per weigh. From 20 to 25 immature copepodites or small cladocerans constituted one sample, but 40 copepod nauplii were required to generate 5 μg net weight.

The relationship between length (μm) and dry weight (μg) was fitted to the equation $W = aL^b$ using the formula $\log W = \log a + b \log L$ (Vann 1972), which enabled us to use linear regression to determine the values of a and b. Zooplankters of a given taxon used to calculate a regression equation were collected at the same time and sempling site.

The results of this study are presented elsewhere (Boucherle 1977 and Culver et al. 1980) but will be summarized here. The lengths chosen for copepods were designed to correspond to identifiable instars, so information on the dry weights of individual stages (Table 2) is available from the

TABLE 2. Lengths and weights for selected copepod stages and taxa in Lake Erie.

TAXON AND STAGE	LENGTH (μm)	WEIGHT (μg)	n
Cyclopoid nauplii			
NI	144	.096	120
NII	198	.160	120
NIII	198	.200	120
NIV	234	.203	120
NV	270	.382	120
NVI	315	.405	80
Cyclops bicuspidatus thomasi			
CI	434	.97	45
CII	471	1.30	15
CIII	525	1.50	30
CIV	597	2.73	17
CV	706	2.95	20
CVI females	724-905	3.4-4.9	67
eggs		.168	306
Cyclops vernalis			
CI	326	.33	45
CII	380	.80	44
CIII	416	.83	45
CIV	489	1.07	45
CV	543	1.43	45
CVI females	597-1086	1.8-8.3	127
CVI males	597- 724	1.5-3.1	70
Mesocyclops edax			
CI	507	.97	30
CII	579	1.20	30
CIII	634	1.77	30
CIV	670	2.73	30
CV	742	2.40	30
CVI females	778-1050	3.8-7.2	120
eggs		.175	300
Calanoid nauplii			
NI	108	.067	120
NII	162	.147	120
NIII	198	.170	120
NIV	243	.280	120
NV	288	.397	120
NVI	342	.450	120
Diaptomid copepodites			
CI	362	.83	45
CII	434	1.13	45
CIII	561	1.30	20
CIV	634	2.33	20

TABLE 2. Lengths and weights for selected copepod stages and taxa in Lake Erie. (Continued).

TAXON AND STAGE	LENGTH (μm)	WEIGHT (μg)	n
Diaptomus minutus CV	652	1.47	20
CVI females	706-851	1.97-3.55	102
D. oregonensis CV	724	3.23	30
CVI females	760-1176	3.84-8.66	104
CVI males	778- 815	4.33-4.80	50
eggs		.214	301
D. siciloides			
CVI females	959-1176	4.75-10.5	77
CVI males	724-1032	3.45-7.47	110

data. Note that the adult copepods had a range of lengths and corresponding weights, so it is necessary to measure adult copepods to determine weights.

The range in lengths included in the regressions, values of a and b, and the residual mean square and correlation coefficients from the regressions are listed for Copepoda in Table 3, and for Cladocera in Table 4. These coefficients were then used in the computer program in the equation $W = aL^b$ to determine the biomass (dry weight) of each individual zooplankter taxon in the samples from Lake Erie and in the Bay of Quinte, Lake Ontario. These species are common to all the Great Lakes, and to many other North American lakes and ponds as well, so we propose the regression equations will be of great utility to other researchers.

Estimation of biomass of rotifers is made difficult by their small size, and we have not attempted to generate precise weights for these taxa. It would be extremely useful in the future to collect and weigh representatives of the many taxa of rotifers present in the Great Lakes.

APPLICATIONS OF THE PRODUCTIVITY PROGRAM TO GREAT LAKES ZOOPLANKTON DATA

To date we have calculated the productivity of zooplankton in the Bay of Quinte, Lake Ontario, for a study of nitrogen and phosphorus loading effects on productivity; in some enclosures in the Bay of Quinte to examine the effect of a potentially toxic substance, nonionic detergent, on zooplankton productivity; in Lake Erie during the 1970 field year in a study of crustacean zooplankton productivity; in the Western Basin of Lake Erie in a study of the contribution of rotifers to Lake Erie zooplankton productivity; and we have almost completed the computer coding of data from a 1948-1949 study of crustacean abundance in the Western Basin of Lake Erie which will allow us to compare productivity at that time with subsequent periods in the lake's

Table 3. Coefficients for length-weight relationships in the form $W = aL^b$ for Lake Erie Copepoda.

The equations use length in μm and generate dry weights in μg.
(RMS = residual mean square, r = correlation coef.)

TAXA	RANGE IN LENGTHS μm (number of weights)		b±95%c.l.	a	RMS	r
Calanoid nauplii NI-NVI	108-342	18	1.7064±0.1259	2.287×10^{-5}	0.0035	0.98
Diaptomus copepodites I-IV	362-634	18	1.7034±0.1342	3.563×10^{-5}	0.0038	0.94
Diaptomus minutus Lilljeborg						
non-ovigerous females CV-CVI	652-851	15	3.8564±0.0916	1.985×10^{-11}	0.0018	0.98
Diaptomus oregonensis Lilljeborg						
males CV-CVI	724-815	7	2.3482±0.1401	6.986×10^{-7}	0.0545	0.80
non-ovigerous females CV-CVI	724-1176	15	1.9604±0.0797	8.141×10^{-6}	0.0014	0.97
Diaptomus siciloides Lilljeborg						
non-ovigerous females CVI	959-1176	14	3.8498±0.0451	1.661×10^{-11}	0.0004	0.98
ovigerous females CVI	996-1267	14	2.3701±0.0924	1.966×10^{-7}	0.0018	0.98
males CVI	724-1032	14	2.6484±0.0865	8.880×10^{-8}	0.0016	0.97
Cyclopoid nauplii NI-NVI	144-315	18	1.6349±0.2523	3.234×10^{-5}	0.0142	0.87
Cyclops bicuspidatus thomasi S. A. Forbes						
non-ovigerous females CI-CVI	434-905	18	1.9347±0.1719	8.904×10^{-6}	0.0066	0.94
Cyclops vernalis Fischer						
non-ovigerous females CI-CVI	326-1086	28	2.5563±0.1975	1.516×10^{-7}	0.0092	0.98
males CI-CVI	326-724	22	2.5320±0.2264	1.740×10^{-7}	0.0118	0.94
Mesocyclops edax S. A. Forbes						
non-ovigerous females CI-CVI	507-1050	26	2.8945±0.2057	1.380×10^{-8}	0.0099	0.95

Table 4. Coefficients for length-weight relationship in the form $W = aL^b$, for Great Lakes Cladocera. The equations use length in μm and generate dry weights in μg (RMS = residual mean square)

TAXA	RANGE IN LENGTHS μm (number of weights)		b±95%c.l.	a	RMS	r
Daphnia galeata mendotae Birge						
non-ovigerous females						
standard length	362-1810	28	1.5302±0.1963	2.806×10^{-4}	0.0091	0.97
total length	471-2172	28	1.5644±0.2156	1.520×10^{-4}	0.0110	0.96
ovigerous females						
standard length	905-1629	13	1.6626±0.0130	1.661×10^{-4}	0.0001	0.97
total length	1176-1991	13	2.0317±0.0074	7.186×10^{-6}	0.0001	0.96
Daphnia retrocurva Forbes						
males - total length	495-594	11	3.8329±1.606	7.310×10^{-1}	0.0260	0.62
non-ovigerous females						
standard length	326-1448	24	2.7552±0.1593	4.095×10^{-8}	0.0050	0.99
total length	398-1810	24	2.6807±0.1402	3.435×10^{-8}	0.0046	0.99
ovigerous females						
standard length	905-1629	14	2.4502±0.0704	3.995×10^{-7}	0.0010	0.99
total length	1176-1991	14	2.7601±0.0933	2.234×10^{-8}	0.0018	0.98
Bosmina longirostris O. F. Muller						
non-ovigerous females	217-434	15	2.2291±0.0870	3.644×10^{-6}	0.0018	0.98
ovigerous females	326-416	15	1.7892±0.0750	3.370×10^{-5}	0.0012	0.92
Eubosmina coregoni Baird						
non-ovigerous females	272-543	17	2.3371±0.1451	2.135×10^{-6}	0.0046	0.96
ovigerous females	362-634	14	2.3321±0.0899	2.724×10^{-6}	0.0017	0.98
Diaphanosoma leuchtenbergianum Fischer						
non-ovigerous females	313-525	15	1.0456±0.0617	3.701×10^{-3}	0.0008	0.95
Leptodora kindtii Focke						
non-ovigerous females	2268-6804	17	1.8730±0.1295	3.752×10^{-6}	0.0037	0.99
Chydorus sphaericus						
non-ovigerous females	219-310	8	1.9796±0.2213	1.621×10^{-5}	0.0014	0.96
Ceriodaphnia lacustris						
non-ovigerous females	329-548	13	1.9763±0.2962	4.737×10^{-6}	0.0066	0.90

history. Each of these applications of the productivity program will be discussed in separate sections below.

NITROGEN AND PHOSPHORUS LOADING AND ZOOPLANKTON PRODUCTIVITY IN THE BAY OF QUINTE

Zooplankton were sampled weekly from a series of six enclosures in the Bay of Quinte, Lake Ontario, and from the Bay itself. Four enclosures received additional P, or P + N such that the loading rates equalled those of the Bay of Quinte. The remaining enclosures served as controls. Secondary productivity was calculated for samples from April to October, 1974. We examined the effect of different P and N loading rates on zooplankton productivity and on the relative productivity by major taxa of zooplankton. These were compared with chlorophyll a concentrations and algal counts to determine the major determinants of zooplankton production in a eutrophic part of Lake Ontario.

Relative contribution of the major groups of zooplankton to each day's productivity was usually Cladocera > Copepoda >> Rotifera (Table 5). The exceptions, Enclosures 4 and 6, may be explained by the fact that rotifer productivity generally increased in the fall and these two enclosures (and #5) were not operative until 17 July. Rotifers of the genus Polyarthra were the primary contributors to the large rotifer productivity in these enclosures. In general, Daphnia galeata mendotae was the most important producer in the enclosures, with Bosmina longirostris and Eubosmina coregoni increasingly important in the Bay of Quinte where fish predation essentially eliminated large cladocerans like D. g. mendotae.

Zooplankton productivity was seldom different among the three treatments, despite the wide variation in productivity observed. One exception was the peaks of production in Enclosure 1 in July due primarily to D. g. mendotae

TABLE 5. Seasonal contribution of Cladocera, Copepoda and Rotifera to the production in enclosures 1-6 and in the Bay of Quinte, 1974.

Station (treatment)	Period	% of Total Production		
		Cladocera	Copepoda	Rotifera
1 (C)	24 Apr-18 Sep	76.6	21.3	2.1
2 (+P)	24 Apr-18 Sep	67.7	31.1	1.2
3 (+N+P)	24 Apr-18 Sep	71.6	26.1	2.3
4 (C)	17 Jul- 9 Oct	48.6	34.4	17.0
5 (+P)	17 Jul- 9 Oct	59.4	34.3	6.3
6 (+N+P)	17 Jul- 9 Oct	31.4	31.4	37.2
Bay of Quinte	1 May-18 Sep	74.6	16.7	8.7

(Fig. 2). This was despite a major increase in chlorophyll (Fig. 3) and algal cell volume in August (Fig. 4) in the enclosure that received both N and P. Nitrogen and Phosphorus additions did not consistantly increase zooplankton productivity and never were as important as internal loading of these nutrients. Zooplankton productivity appears to have followed non-bluegreen algae biomass (Fig. 4) better than the chlorophyll concentration, probably because of the unsuitability of bluegreen algae in general as food for zooplankton. In mid-summer, addition of nitrogen seemed to encourage the relative growth of non-fixers of nitrogen among the Cyanophyta, but neither form of bluegreen algae seemed to stimulate productivity of zooplankton.

Further discussion on these samples can be found elsewhere (Culver and DeMott 1978, Culver and Lean 1980, Culver et al. 1980), but it is important to emphasize that zooplankton productivity did not appear to be directly related to either phosphate concentration, phosphorus loading, or chlorophyll. Internal cycling of phosphorus and the taxonomic composition of the phytoplankton are probably among the most important factors after temperature.

Secondary Productivity as an Assay for Effects of a Toxic Substance

Secondary productivity should be sensitive to the addition of toxic substances since it is determined by growth and reproductive output, both of which may be affected by toxic materials. Accordingly, we used three of the enclosures to determine the effects of a nonionic detergent (nonylphenol ethoxylate) on the zooplankton. Enclosure 4 was a control, Enclosure 5 received 0.6 mg/l Nonionic detergent (NID) and Enclosure 6 received 3.0 mg/l NID, on 24 September 1974. We then continued to follow the productivity of the zooplankton in the three enclosures until 9 October.

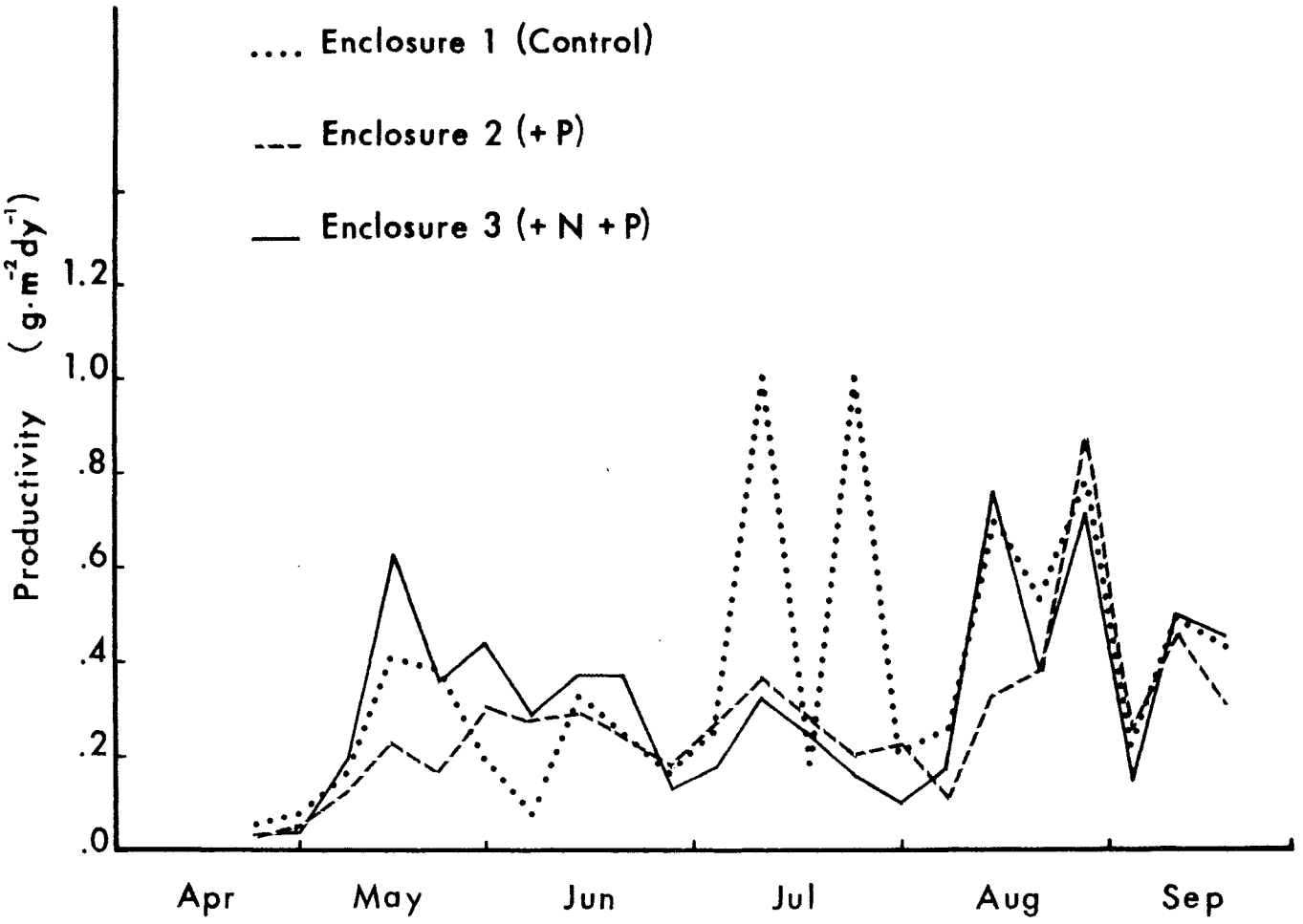

Figure 2. Productivity in three enclosures in the Bay of Quinte, Lake Ontario, 1974.

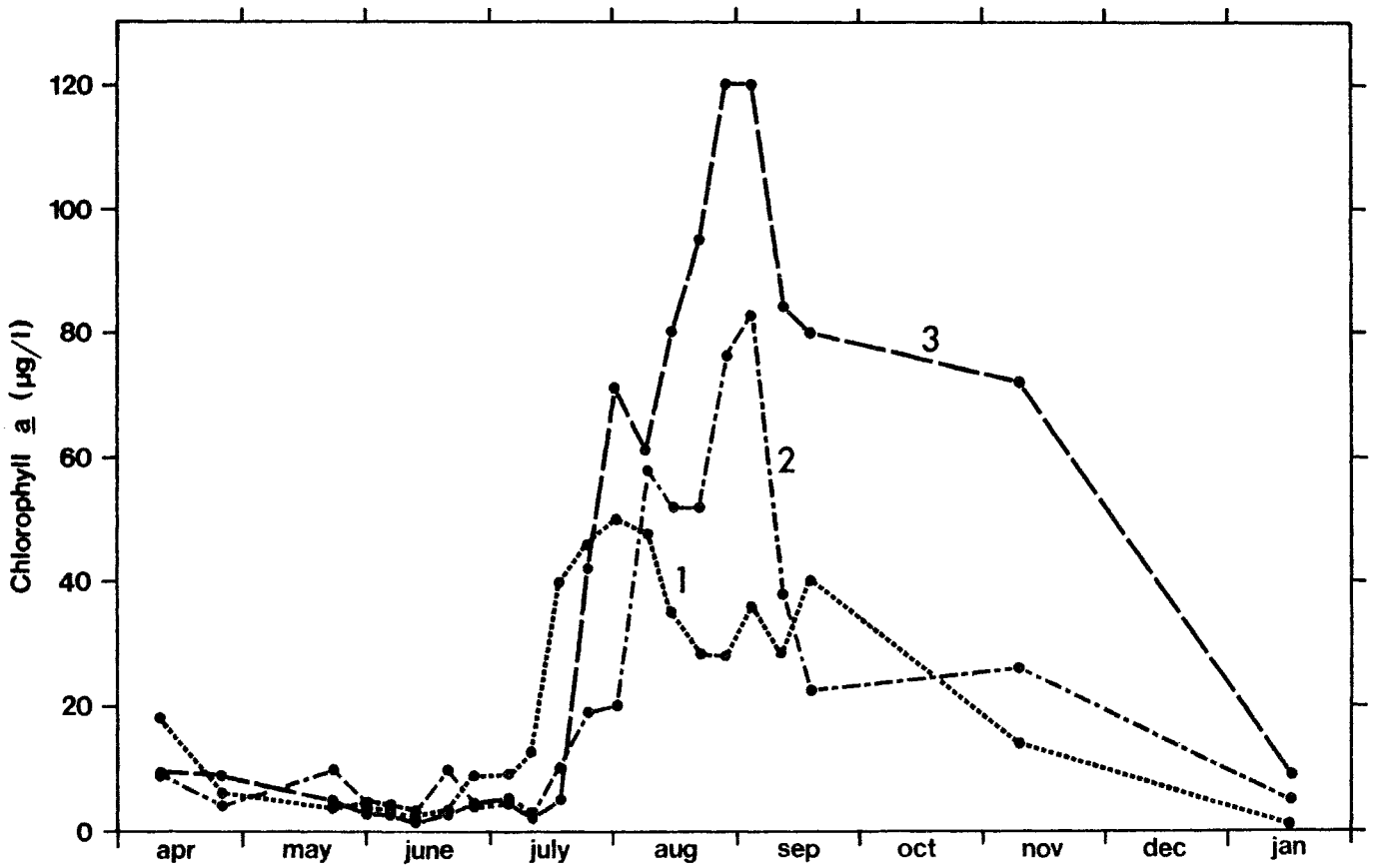

Figure 3. Concentration of chlorophyll a for the three enclosures in the Bay of Quinte, Lake Ontario, 1974. Enclosure 1 = control, Enclosure 2 = +P, Enclosure 3 = +N+P.

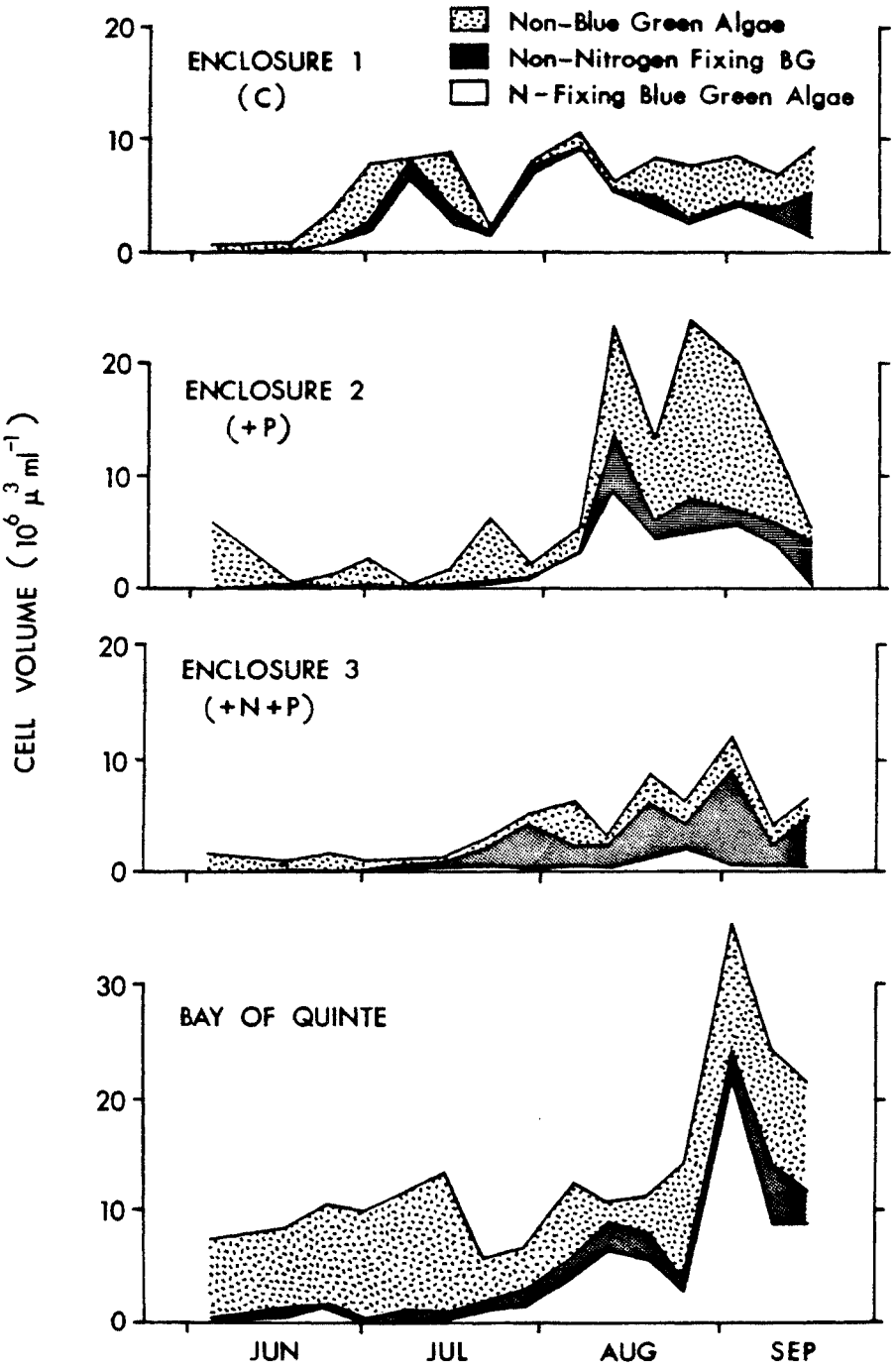

Figure 4. Volumes of phytoplankton in three enclosures and the Bay of Quinte, Lake Ontario, 1974.

Our analysis of biomass changes showed that all three enclosures declined after the addition of NID to two of them (Table 6). The decrease in Enclosure 6 was 80%. The patterns of decrease in biomass in the lower NID addition (Enclosure 5) and the control (Enclosure 4) were less and there is no reason to believe that the decrease in Enclosure 5 was any more than would be expected from the cooling of the water in September and October. Much of the change in biomass in Enclosure 6 was due to a decrease in the abundance of Bosmina longirostris (2701 mg/m^2 to 797 mg/m^2) and Polyarthra spp. (5169 mg/m^2 to 202 mg/m^2). In the control enclosure, the same species declined from 2701 mg/m^2 to 1131 mg/m^2 and from 5169 mg/m^2 to 1419 mg/m^2 respectively. Cyclops vernalis decreased by 33% in the control and by 50% in Enclosure 6 over the same time period.

At the same time, the secondary productivity decreased by a factor of two in the low NID enclosure, and by a factor of seven in the high NID enclosure, while the control enclosure had an increase of one and one half times the pre- addition level. The effect of the NID is also represented by comparison of the ratio of productivity to biomass, which measures the fraction of the standing crop that is produced each day (Table 6). Both enclosures with NID had a decrease in P/B, whereas the control enclosure P/B actually increased from 18 September to 26 September.

There were two factors that confounded the NID study unnecessarily. In the first place, the experiment was performed on enclosures that had been used in the nitrogen and phosphorus enrichment study referred to above, although no enrichment was performed after the addition of the NID. Enclosure 6 had received N + P, while #5 had received + P from July to mid-September. Enclosures 5 and 6 thus were not fully equivalent to Enclosure 4 at the beginning of the experiment. Secondly, the experiment was performed at the

TABLE 6. Effect of non-ionic detergent on biomass, productivity, and productivity + biomass ratio (P/B) in the Bay of Quinte, Lake Ontario, 1974. Non-ionic detergent (nonylphenol ethoxylate) was added to two of the enclosures on 24 September 1974.

Date	Temperature	Treatment	Biomass (g/m^2)	Productivity ($g/m^2/day$)	(day^{-1})
18 Sep 74	18.10°C	Control	3.35	0.26	0.078
		(NID)	3.46	0.60	0.174
		(NID)	8.95	1.28	0.144
26 Sep 74	14.90	Control	3.81	0.41	0.107
		NID 0.6 mg/1	4.20	0.30	0.071
		NID 3.0 mg/1	1.83	0.18	0.096
3 Oct 74	11.70	Control	2.31	0.14	0.060
		NID 0.6 mg/1	3.09	0.16	0.052
		NID 3.0 mg/1	1.43	0.15	0.104
9 Oct 74	11.00	Control	1.56	0.07	0.042
		NID 0.6 mg/1	2.89	0.11	0.039
		NID 3.0 mg/1	1.46	0.13	0.087

end of the summer when declining temperatures (Table 6) also affected the growth and reproduction of the zooplankton. Despite these design problems, the productivity calculations and biomass estimates based on size-frequency measurements showed the zooplankton were sensitive to NID at both 0.6 mg/l and 3.0 mg/l, and that this sensitivity was observable in copepods, cladocerans, and rotifers. Future experiments of this type should be done with enclosures started at the same time during a period of relative constant temperature, unless the effects of temperature change wish to be examined specifically.

ZOOPLANKTON PRODUCTIVITY IN LAKE ERIE, 1970

Productivity of the Crustacean Zooplankton

As mentioned previously, the similarity of species composition among the Laurentian Great Lakes makes the productivity program useful in all of them. A primary goal of this work has been to evaluate the variation in zooplankton productivity in Lake Erie during its progressive increase in nutrient loading. A series of ten lakewide cruises made in 1970 by the Canada Centre for Inland Waters provided data from ice out in the spring to December from 30 stations (Fig. 5). CCIW analyzed water quality at each of the stations, including various forms of phosphorus, nitrogen, and inorganic carbon as well as reactive silicate, chlorophyll, temperature, transparency, algal species, crustacean zooplankton species, and primary productivity (Bean 1980). Much of the results of the water quality studies has been published (Burns 1976, Burns et al., 1976, Sly 1976 and Munawar and Burns, 1976), so our studies build on their results.

Zooplankton analyses (Watson 1976) were limited to abundances of crustaceans, so we counted eggs, did size-frequency determinations, and measured the size at maturity for the crustacean zooplankton using samples

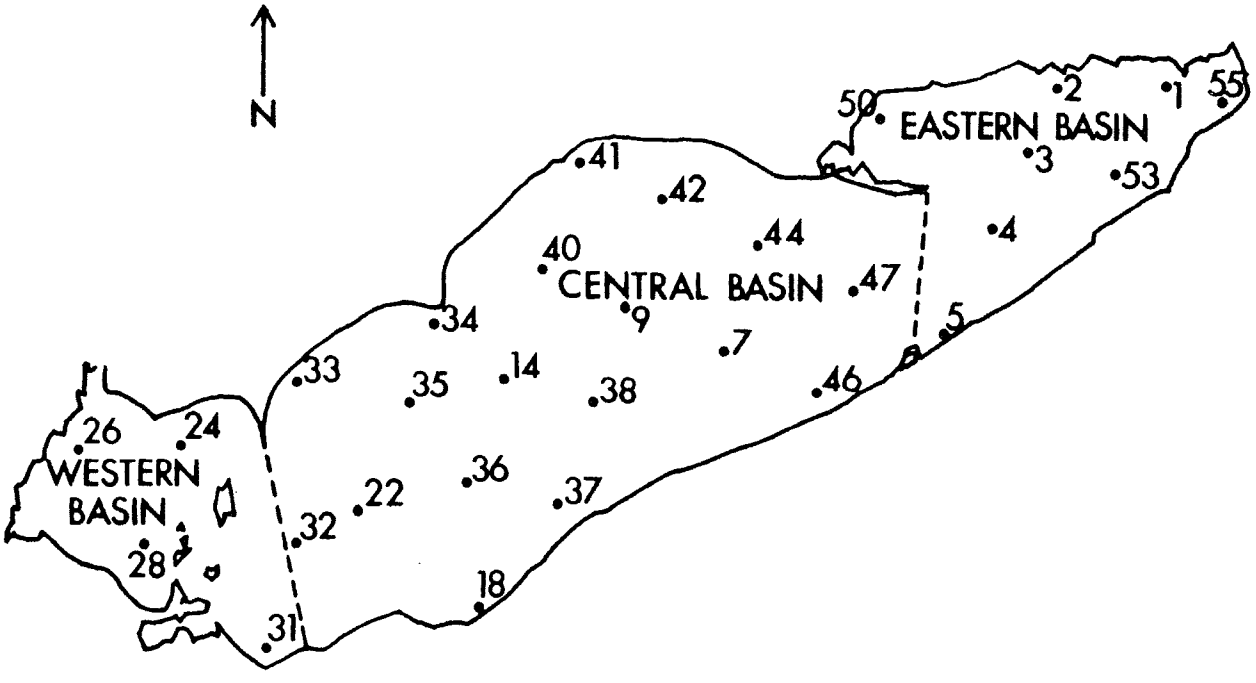

Figure 5. Chart showing sampling stations in Lake Erie used for the 1970 field season.

provided by Dr. Nelson Watson, CCIW(Bean 1980). Culver and Dorazio (1980) enumerated eggs and adults of the rotifers from the Western Basin samples in order to evaluate the contribution of rotifers to the secondary productivity of the lake.

The highest crustacean productivity occurred in the Western Basin (Table 7) on a $mg/m^3/day$ basis. In order to compare on a $mg/m^2/day$ basis, it is necessary to multiply the productivities (and biomasses) by the average depths of the basins, which are 8 m for the Western Basin, 15 m for the Central Basin and 25 m for the Eastern Basin. These productivity values are lower than those found by Culver and DeMott (1978) for single stations in the nearshore zones of Lakes Erie and Ontario, due primarily to the fact that most of the stations in the 1970 cruises were in deeper water, where the productivity is certainly lower than it is in shore.

The P/B ratios are lower than those found by Culver and DeMott (1978) too, indicating that the turnover times for biomass (B/P) were longer in the offshore waters than they were in the nearshore. The P/B ratios were much higher in the summer than they were in spring or fall, a result of higher temperatures and food availability. The value of 0.193 day^{-1} in early July for the Western Basin implies that the biomass was replaced every 5.2 days. Under that circumstance, the period between cruises (4 weeks) was too long to adequately sample the changes in zooplankton productivity occurring in the lake at that time of the year.

The relative contribution of different species to the crustacean productivity in 1970 varied seasonally. In spring, Cyclops bicuspidatus thomasi was the dominant producer, but cladocerans were more important during the rest of the year. Daphnia retrocurva was generally the most important producer in the summer, while Bosmina longirostris was the

TABLE 7. Productivity and Biomass in Lake Erie, 1970. To turn these volumetric estimates to mg/m^2, the values for B and P must be multiplied by the average depth of the basins: WB = 8m, CB = 15m, EB = 25m.

Basin	Cruise	Dates	Biomass (mg/m^3)	Productivity (mg/m^3/Day)	P/B
Western		April 7-11	72.12	0.09	0.001
Central	1	April 7-11	43.53	0.13	0.003
Eastern		April 7-11	45.32	0.11	0.002
Western		May 6-10	307.40	0.81	0.003
Central	2	May 6-10	49.18	0.30	0.006
Eastern		May 6-10	30.24	0.08	0.005
Western		June 2-6	621.48	12.19	0.020
Central	3	June 2-6	543.03	14.74	0.027
Eastern		June 2-6	195.68	3.74	0.019
Western		July 3-7	401.89	77.41	0.193
Central	5	July 3-7	458.14	21.71	0.047
Eastern		July 3-7	528.14	17.16	0.032
Western		July 28-Aug. 1	1127.17	171.59	0.152
Central	6	July 28-Aug. 1	253.27	8.30	0.033
Eastern		July 28-Aug. 1	215.61	5.92	0.027
Western		Aug. 25-29	194.24	23.72	0.122
Central	7	Aug. 25-29	142.29	6.68	0.047
Eastern		Aug. 25-29	106.00	3.38	0.032
Western		Sept. 23-27	156.57	8.62	0.055
Central	9	Sept. 23-27	93.59	9.36	0.100
Eastern		Sept. 23-27	77.84	1.59	0.020
Western		Oct. 21-25	34.20	1.90	0.056
Central	10	Oct. 21-25	48.50	1.46	0.030
Eastern		Oct. 21-25	32.33	0.60	0.019
Western		Nov. 25-30	64.61	1.37	0.021
Central	11	Nov. 25-30	60.87	0.59	0.010
Eastern		Nov. 25-30	38.40	0.22	0.006
Western		Dec. 14-18	47.06	0.79	0.017
Central	12	Dec. 14-18	36.18	0.33	0.009
Eastern		Dec. 14-18	18.80	0.08	0.004

dominant producer in the fall. Other crustacea were important occasionally, depending upon the basin (Fig. 6). Eubosmina coregoni, Daphnia galeata mendotae, and Chydorus spaericus were all important at various times.

Bean (1980) performed a principle axis factor analysis on temperature, total phosphorus, soluble reactive phosphorus, total filterable phosphorus, ammonia, nitrite + nitrate, reactive silicate, chlorophyll a, primary productivity, and secondary productivity using our secondary productivity values and the data provided by the Canada Centre for Inland Waters. The productivity of crustacean zooplankton was correlated with temperature, some form of phosphorus (depending on season), and either primary productivity or chlorophyll a. While these results are not surprising, it should be noted that sampling a system every 4 weeks should mask much of the dynamics of the rapid turnover of the plankton community, especially if lag times between phytoplankton growth and zooplankton productivity occur. These analyses show that zooplankton productivity at a given time of year is correlated with temperature, phosphorus, and phytoplankton collected at the same time; that is, the response of the zooplankton to phytoplankton productivity, phosphorus and temperature is so rapid that the correlations still hold even without allowing for lag times. In the spring, secondary productivity was negatively correlated with primary productivity, indicating that the organisms carrying out most of the zooplankton growth (Cyclops bicuspidatus thomasi) were not dependent upon or could not utilize the algae growing at that time. Adult C. b. thomasi are predaceous, which might in part explain the lack of correlation, but not the negative correlation obtained. Should a more precise analysis of factors affecting secondary productivity be required, it is evident the analysis will have to be based on samples taken at least weekly, which will of necessity limit it to a smaller

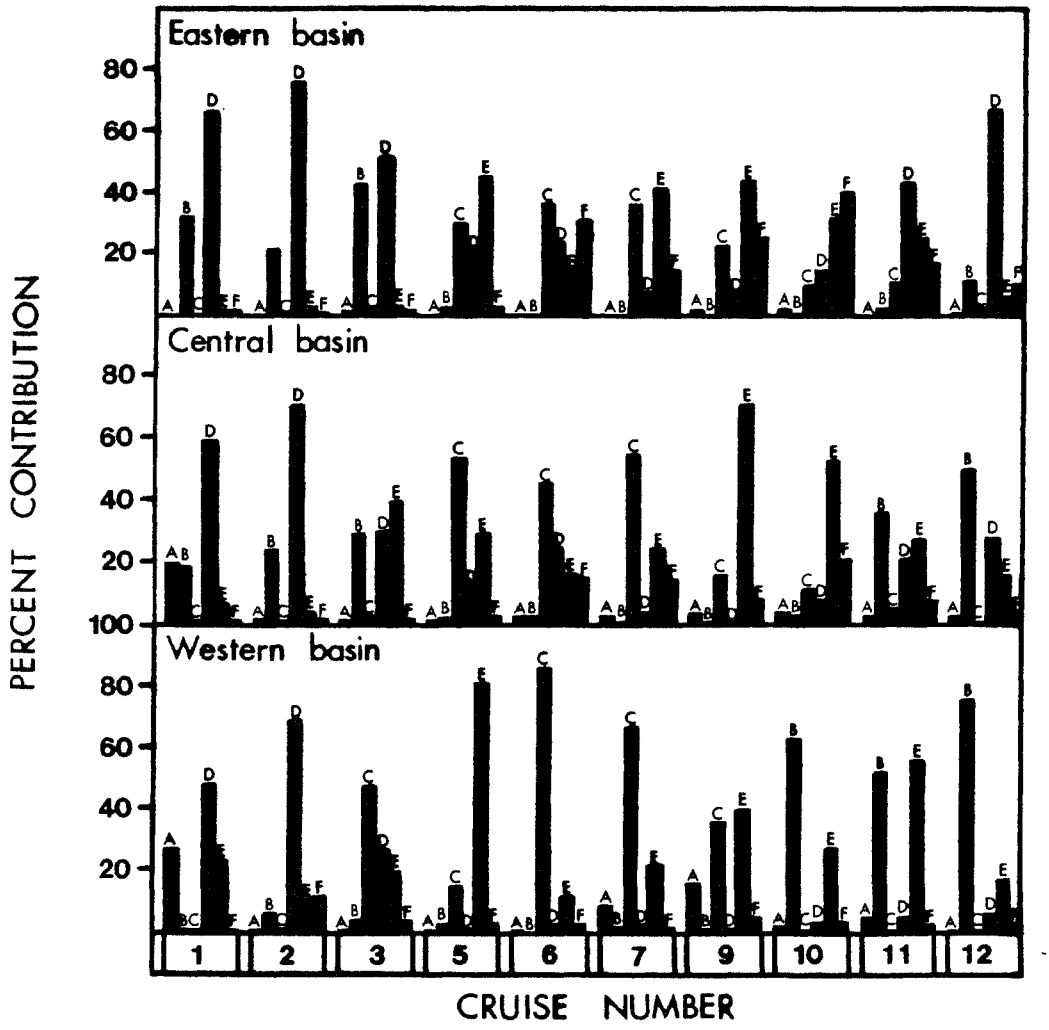

Figure 6. Relative contribution of major taxa to the zooplankton productivity of each of the three basins of Lake Erie, 1970.

number of stations than the 30 sampled in this study.

Productivity of Rotifers in the Western Basin, Lake Erie, 1970

As mentioned above, rotifers were not identified or counted in the CCIW study, so we performed enumerations on the samples from the Western Basin samples in order to determine the relative contribution of the rotifers to the biomass and productivity of the zooplankton in 1970. Because many of the eggs were not attached to the adult rotifers in the samples, we counted the total number of eggs/m^3 and apportioned them over the species found in the sample (Table 8) according to the relative abundance of those species (Culver and Dorazio 1980). Biomass of the rotifers was calculated using data from D. Larson (Personal Communication) who measured length, height and width of each species and then calculated the volume of the species using the formula for the volume of the shape (e.g. oblate spheroid) that was most similar to the shape of the particular taxon. She then assumed a specific gravity of 1.0 g cm^{-3} and a percentage of the dry weight of ten percent for all taxa to calculate the dry weight per individual.

By combining the results of this study (Culver and Dorazio 1980) with those of Bean (1980) we can assess the overall importance of the Rotifera to the productivity of the zooplankton in Lake Erie during 1970 (Fig. 6, 7 and 8). It is immediately apparent that while the productivity of the rotifers does not match the levels attained by copepods and cladocera at their peak abundances, they are responsible for a major proportion of the productivity in the early spring and late fall in the lake. The early spring bloom may be particularly important to the larval fish that are hatching out in Lake Erie in April, May and June. The current practice of concentrating on the crustacean plankters, ignoring rotifers in Great Lakes studies is simply

TABLE 8. Species of rotifers enumerated from the Western Basin, Lake Erie, 1970.

Asplanchna sp.

Brachionus sp.

Brachionus angularis

Brachionus calyciflorus

Brachionus caudatus

Brachionus havanaensis

Brachionus rubens

Chromogaster sp.

Conochilus unicornus

Filinia terminalis

Kellicottia longispina

Keratella quadrata

Monostyla lunaris

Notholca acuminata

Notholca foliacea

Notholca squamula

Ploesoma sp.

Polyarthra euryptera

Polyarthra major

Polyarthra minor

Polyarthra vulgaris

Pompholyx sulcata

Squatinella sp.

Synchaeta sp.

Synchaeta stylata

Synchaeta assymmetrica

Trichocerca cylindrica

Trichocerca multicrinis

Trichocerca stylata

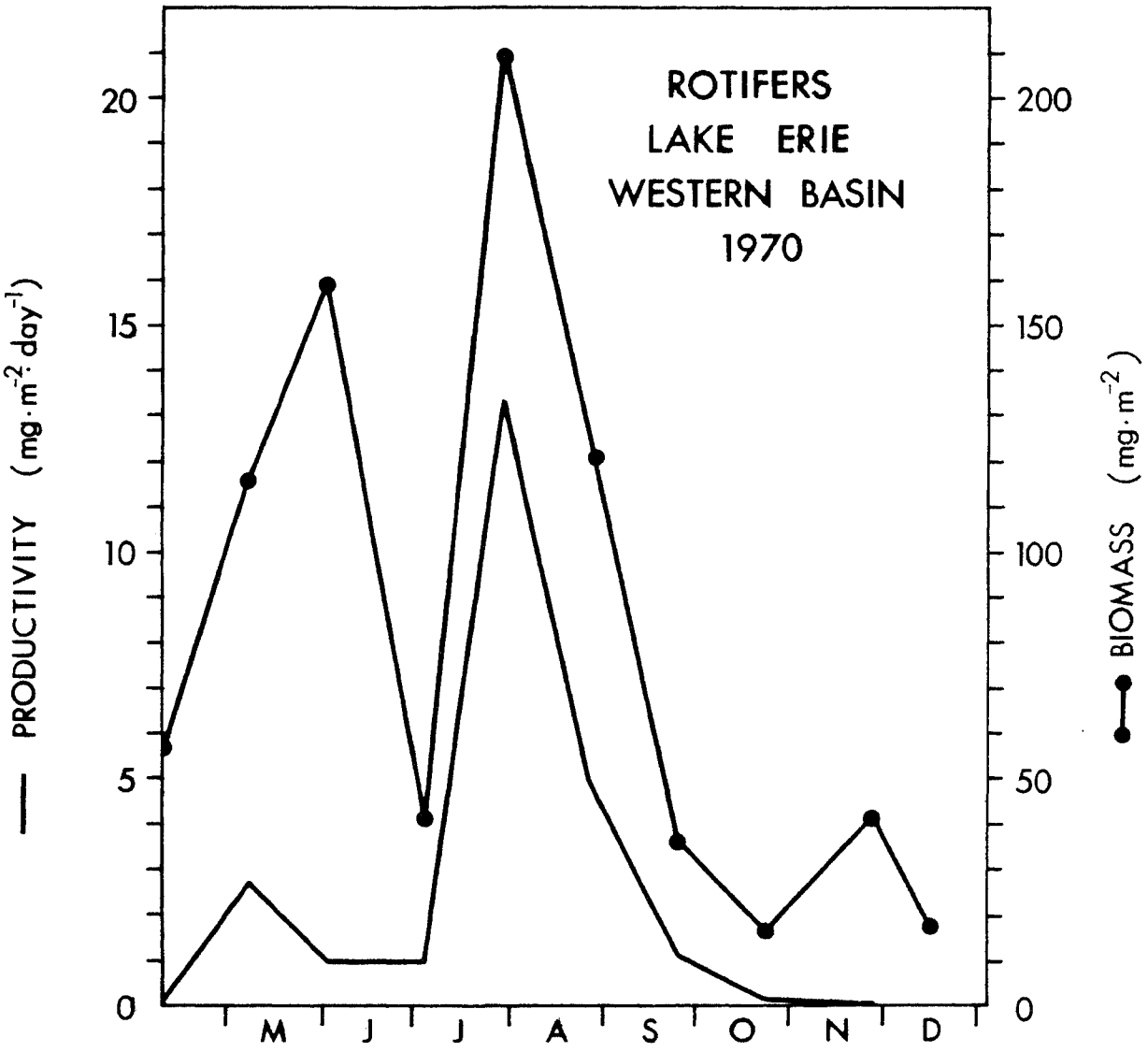

Figure 7. Productivity and biomass of rotifers in the Western Basin of Lake Erie, 1970.

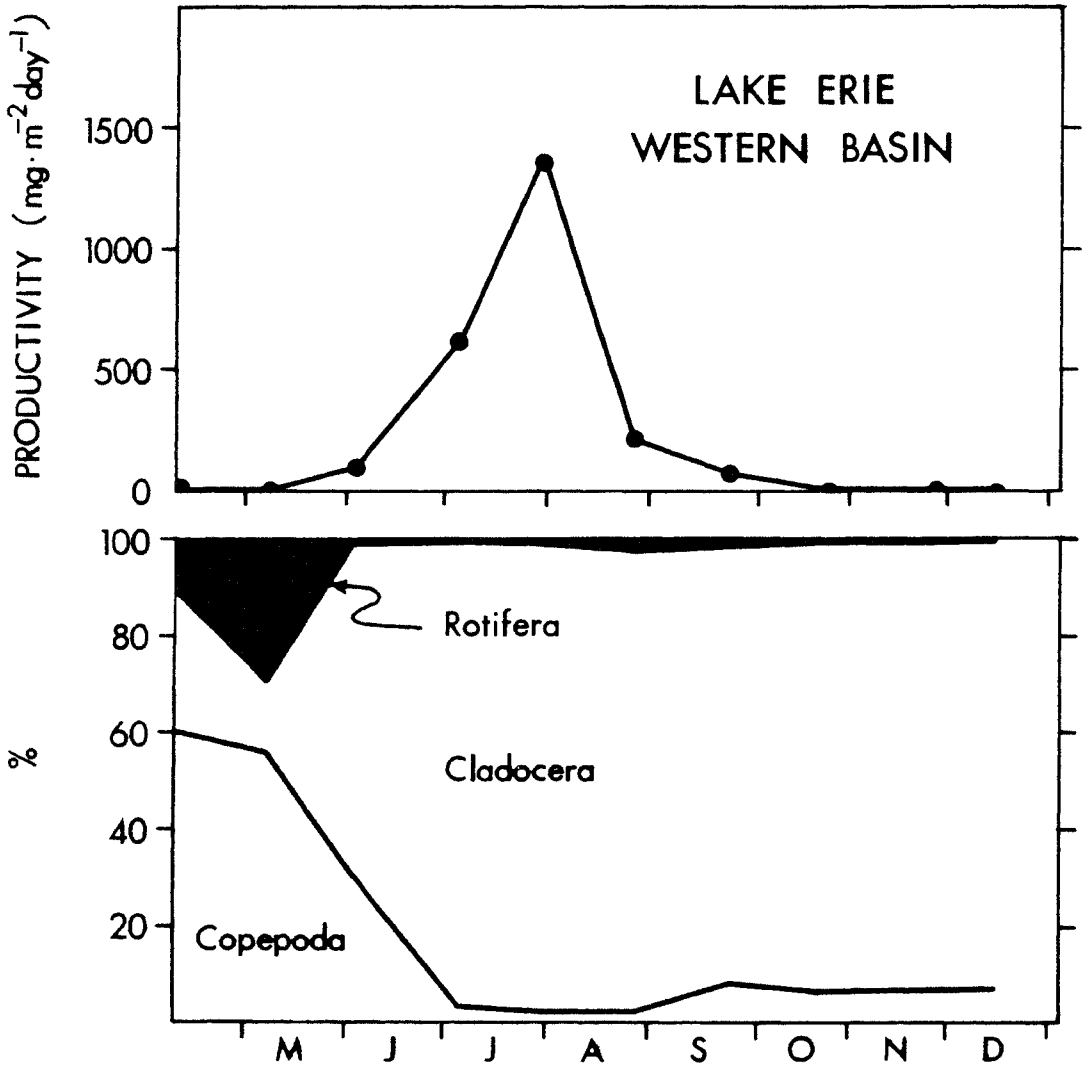

Figure 8. Total zooplankton productivity (upper panel) and relative contribution of major taxonomic groups to zooplankton productivity (lower panel) for the Western Basin of Lake Erie, 1970.

inappropriate if the total flux of energy through the planktonic community is to be estimated.

PRODUCTIVITY OF CRUSTACEAN ZOOPLANKTON IN LAKE ERIE, 1948-1949

It is characteristic of our productivity model that it takes standing crop estimates of zooplankton abundance and predicts what the growth of the population will be over the next twenty-four hours assuming no predation occurs. As such, it is quite easy to estimate secondary productivity from historical data provided temperature measurements, species enumerations, egg counts, and size-frequency data are available. A. S. Bradshaw has made available to us a data set collected from three stations in the Western Basin of Lake Erie near South Bass Island collected with a Juday trap between June 1948 and July 1949. While rotifer counts are unavailable from these samples, Bradshaw did enumerate crustaceans, measure the cladocerans, count eggs from both groups, as well as describe a myriad of other characteristics of the cladocerans present in the samples. The samples were collected in conjunction with algal studies being performed by J. Verduin (1951a, 1951b) and were described briefly by Bradshaw (1964).

At the current time, we have almost finished coding and keypunching the data from Bradshaw's samples, and intend to calculate secondary productivity for the samples within a short time. This will enable us to compare the activity of the zooplankton from another period in the history of eutrophication of Lake Erie, at a time when phosphorus loading was significantly lower than it was in 1970, or is now.

SIZE AT FIRST REPRODUCTION IN CRUSTACEA

As discussed in the methods section, calculation of secondary productivity

in Cladocera required knowing the size at maturity. Our first determinations of size at maturity demonstrated that it was not a constant, but changed seasonally, necessitating a separate estimate for each species on each sampling date. While seasonal changes in size at maturity had been described for copepods previously (Deevey 1960), this is the first time that size at first reproduction was examined seasonally for the entire cladoceran assemblage (Culver 1980). The analyses included the Cladocera in the Bay of Quinte study (1974 field season) and the Cladocera and Copepoda from Lake Erie (1970 field season).

The samples from The Bay of Quinte, Lake Ontario, were collected weekly from the Bay and from the six enclosures discussed previously. Analyses were performed on the Bay samples and on the enclosure samples as two treatments, one with fish predation (the Bay) the other without (the Enclosures). This allowed us to test whether the decrease in size from spring to summer was due to size-selective predation by fish, or whether some other factor was involved. Finally, we compared these results with some data collected by W. R. DeMott at a nearshore station in Lake Erie for the same species of Cladocera.

Cladoceran species occurring in the samples with sufficient frequency to construct length distributions were Bosmina longirostris, Eubosmina coregoni, Ceriodaphnia lacustris, Chydorus sphaericus, Diaphanosoma leuchtenbergianum, Daphnia retrocurva and Daphnia galeata mendotae. Numerical abundance of the various species in the Bay showed a pronounced seasonal pattern (Fig. 9) with some species (e.g. C. lacustris, D. retrocurva, and D. leuchtenbergianum) rare until mid-summer while other species (Eubosmina and Chydorus) were present in varying abundance throughout the year. Abundance patterns inside the enclosures were different from those outside, with D.

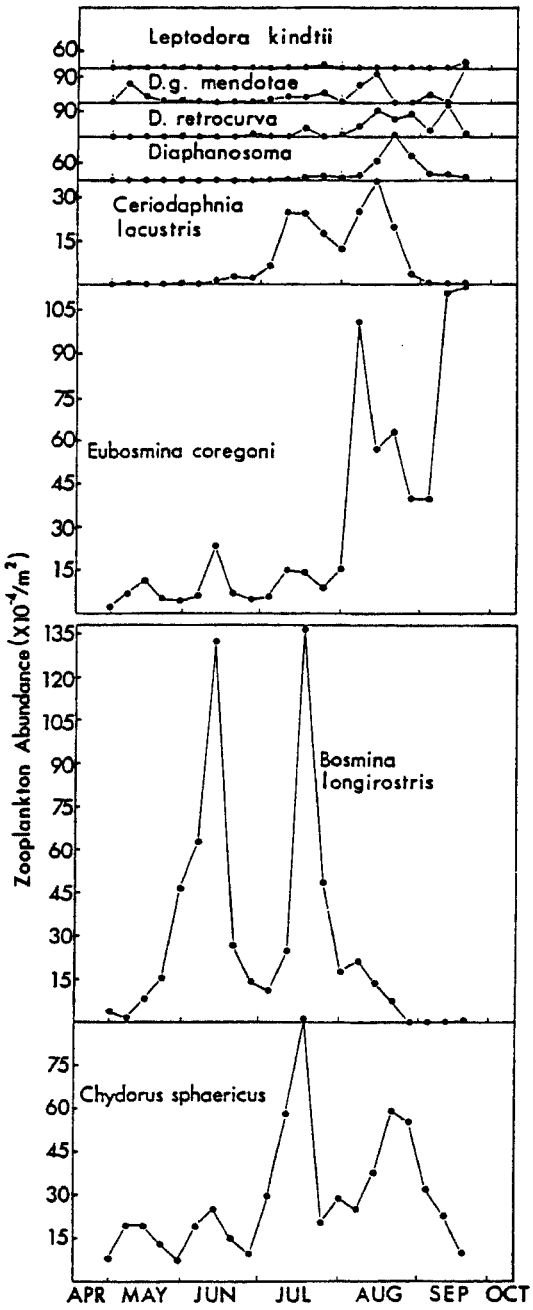

Figure 9. Relative numerical abundance of major cladoceran species in the Bay of Quinte, Lake Ontario, 1974.

galeata mendotae common inside the enclosures throughout the year but scarce in the Bay except for brief periods.

Temperature in the Bay of Quinte was never stratified at the sample site, and thermal patterns inside and outside the enclosures were similar. Temperature patterns show the effects of periods of fair weather which caused rapid temperature increases (Fig. 10).

The cladoceran size at first reproduction, which was determined as the 10th percentile for ovigerous females, showed a general pattern of decrease for all species during summer followed by an increase in late fall (Fig. 11 and 12). There is a slight difference between size at first reproduction and size at maturity, since the former requires the presence of eggs in the brood pouch, while the latter is determined by the development of the ovaries. At a magnification of 100x, many of these individuals were too small to allow observation of the condition of the ovaries, so we determined the sizes of ovigerous individuals for our analyses. The number of measurements available to construct the size at first reproduction (SFR) and neonate lengths for a given date, species and station in the Bay of Quinte ranged from 14 to 300 with a mean of 73. We took 37,791 measurements. The patterns of SFR and neonate length for the two Daphnia species are less regular than those of the other species because total length measurements are sensitive to the development of helmets by these highly cyclomorphotic forms. The greater abundance of large cladoceran forms in the enclosures is reflected in the greater number of observations plotted for these species (Fig. 12) as compared to the Bay samples(Fig. 11). This is a direct effect of fish predation in the Bay on the larger cladoceran species.

Eubosmina coregoni adults from Locust Point, Lake Erie, (open squares marked "e" in Fig. 11) also showed a seasonal decline in SFR but at a much

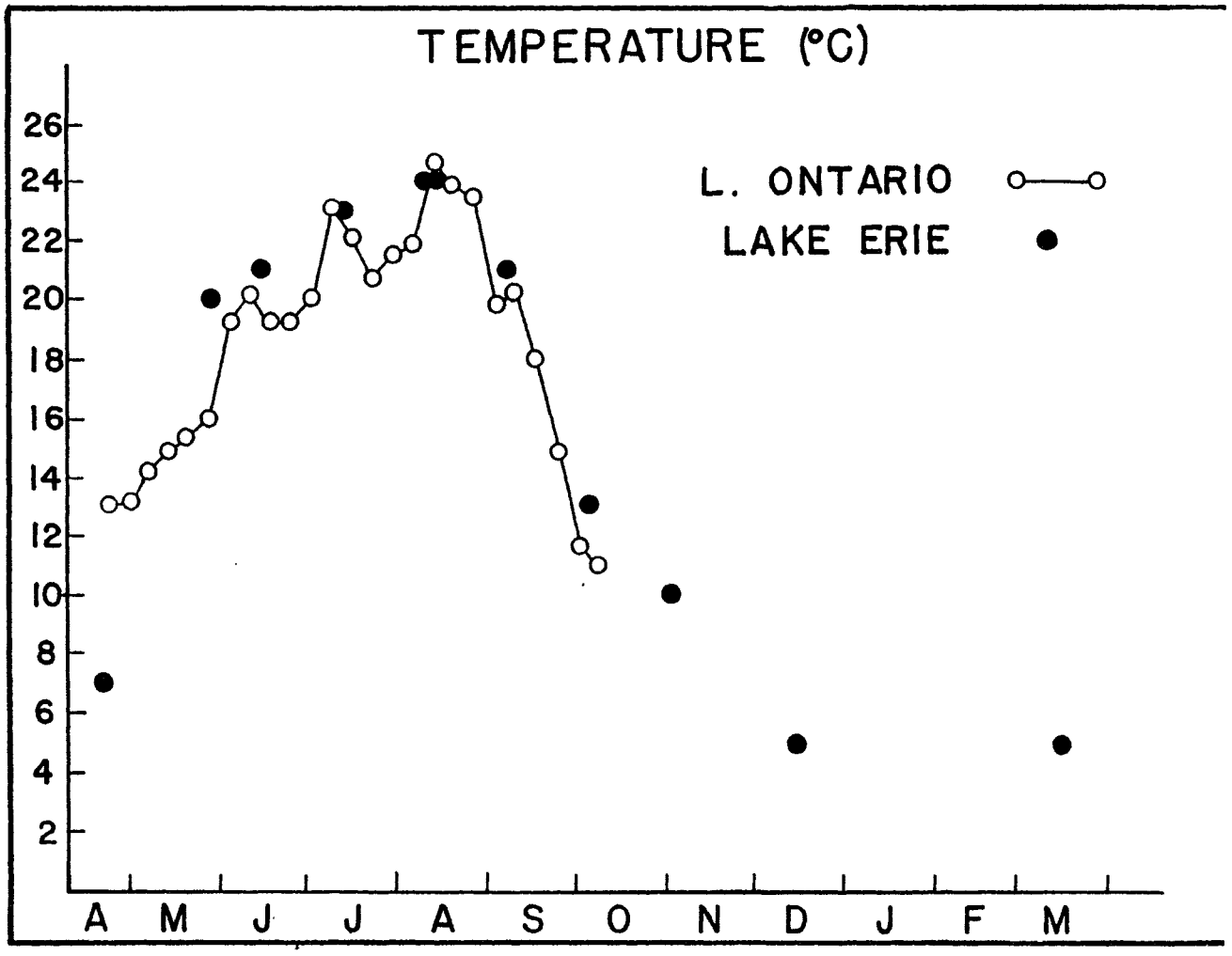

Figure 10. Water temperature in the Bay of Quinte, Lake Ontario, 1974, and at Locust Point, Western Basin Lake Erie, 1975-1976.

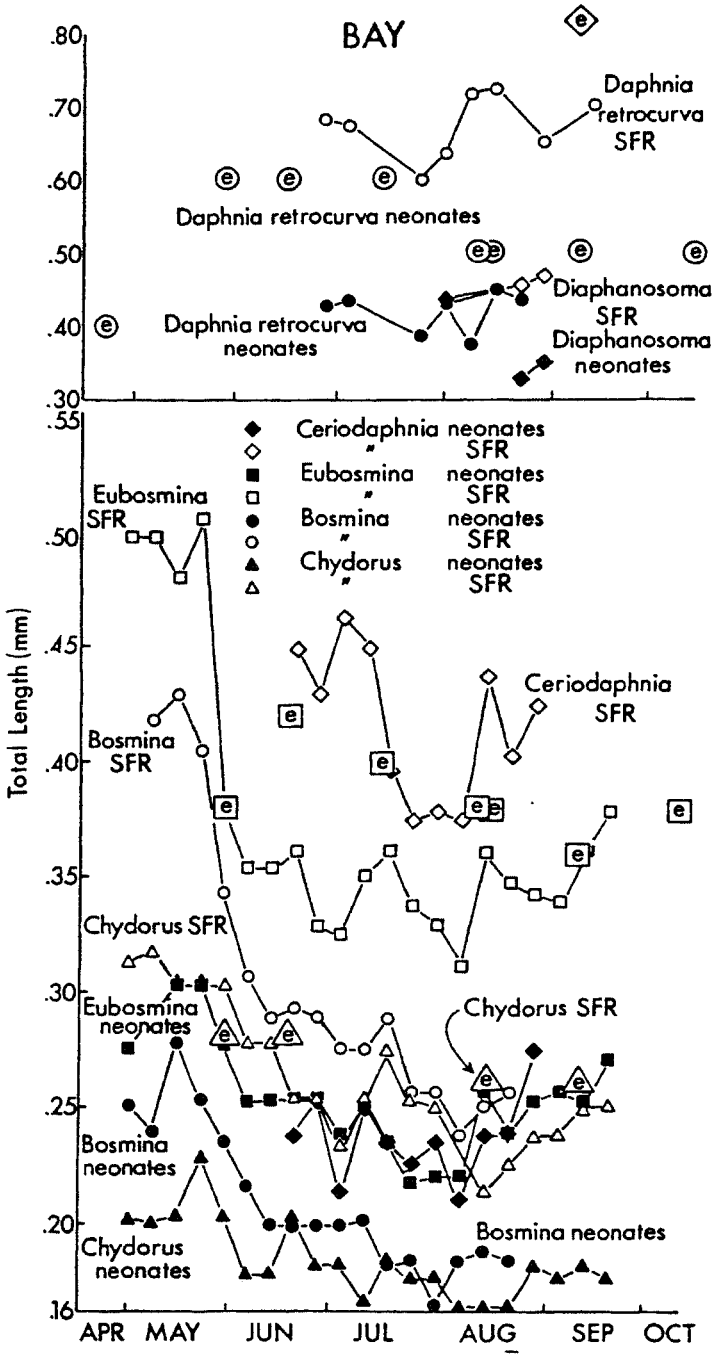

Figure 11. Size at first reproduction and neonate length for major cladoceran species in the Bay of Quinte, Lake Ontario, 1974. Triangles and squares marked "e" in lower panel are from Chydorus and Eubosmina individuals collected at Locust Point, Lake Erie, respectively. Circles marked "e" are Daphnia galeata mendotae neonates, from Lake Erie, whereas the one diamond marked "e" is the size at first reproduction for Diaphanosoma females in Lake Erie on that date.

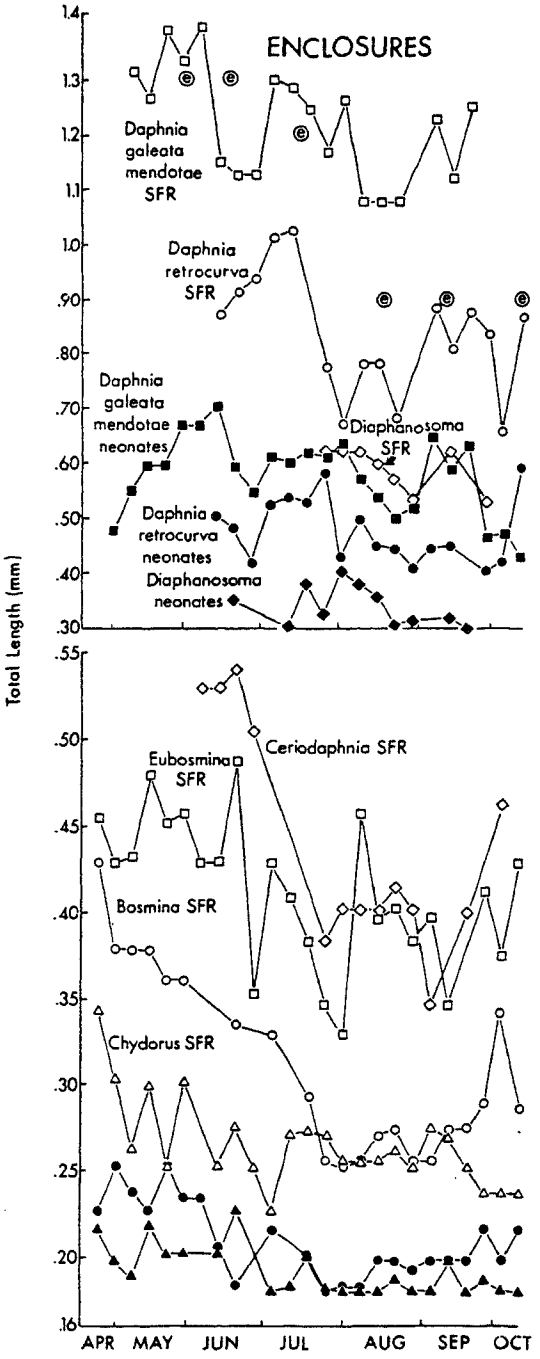

Figure 12. Size at first reproduction and neonate lengths for major cladoceran species occurring in the enclosures in the Bay of Quinte, Lake Ontario, 1974. Circles marked "e" in the upper panel are for Daphnia retrocurva from Locust Point, Western Basin, Lake Erie, 1975.

larger size than for Lake Ontario. Chydorus sphaericus (open triangles marked "e" in Fig. 11) showed a similar pattern. Daphnia retrocurva SFR values were also larger in the Locust Point, Lake Erie, samples than in the Bay of Quinte samples (top panel of Fig. 12, open circles marked "e"). It was surprising to find this difference in SFR seasonal patterns of the two lakes since Lake Erie drains into Lake Ontario and the samples were collected from two similar nearshore stations.

The tandem decrease among SFR and neonate lengths during the spring and summer among all the species is quite striking (Figs. 11 and 12). Species which were rare in the early spring (D. retrocurva, C. lacustris, and D. leuchtenbergianum) all enter at SFRs and neonate sizes intermediate with those species already abundant and then vary with them. The maximum adult sizes obtained by all these species are also discrete and decline seasonally along with SFR and neonate sizes.

The similarity of the SFR values inside and outside the enclosures suggests that the decline in SFR and neonate sizes with increasing temperature is not a direct result of selective predation by fish, because there were no fish in the enclosures. Because fish typically do not eat zooplankters smaller than 1 mm, it is difficult to explain the decline in size by the smallest cladocerans unless the decline of the larger species that are susceptible to predation would cause significant competition with smaller forms when the larger forms decreased in size during the summer. This suggests two interesting aspects of the seasonal change in size. First, that the seasonal change probably was ultimately caused by size-selective predation by fish, but that it currently happens in response to environmental cues, either temperature or some close correlate of it, and that it is therefore a form of cyclomorphosis. Secondly, it suggests that the numerous

species of cladocerans living in Lake Ontario coexist by dividing up resources such as food on some size basis. If the latter is true, we would expect that there would be differences in the sizes of particles eaten by these organisms as a function of their body sizes, with the largest species eating the largest food items. We intend to examine this hypothesis in a future study.

Bean (1980) examined the measurements of cladocerans and copepods from Lake Erie (1970 field season) and found similar patterns to those found by Culver (1980) in the Bay of Quinte, Lake Ontario. The relative sizes of the cladocerans were in the same order as in Lake Ontario, although they were larger as mentioned previously for DeMott's samples from Locust Point, Lake Erie. There was a decline in SFR seasonally in the Lake Erie samples (Fig. 13) although it occurred later in the season than it did in the shallow Bay of Quinte station, which warmed up quickly. The patterns in Lake Erie are plotted for the mean of all stations, which masks some of the differences in rate of warming among the Western, Central, and Eastern Basins in Lake Erie. The stations varied in proximity to shore and in the abundance of planktivorous fish, so it is difficult to compare them directly with the values obtained in the single Bay of Quinte station. Still, the Lake Erie samples show that the phenomenon that had been described only for the nearshore zone of single stations in Lakes Ontario and Erie has now been found to occur in Lake Erie as a whole as well.

Bean (1980) also demonstrated a similar pattern for the major copepod species in Lake Erie (Cyclops bicuspidatus thomasi, Diaptomus minutus, Mesocyclops edax, and Diaptomus oregonensis). He found that the mean adult size of these species varied seasonally and that there was no overlap in size between adults of the two Diaptomus species, which are herbivores, nor

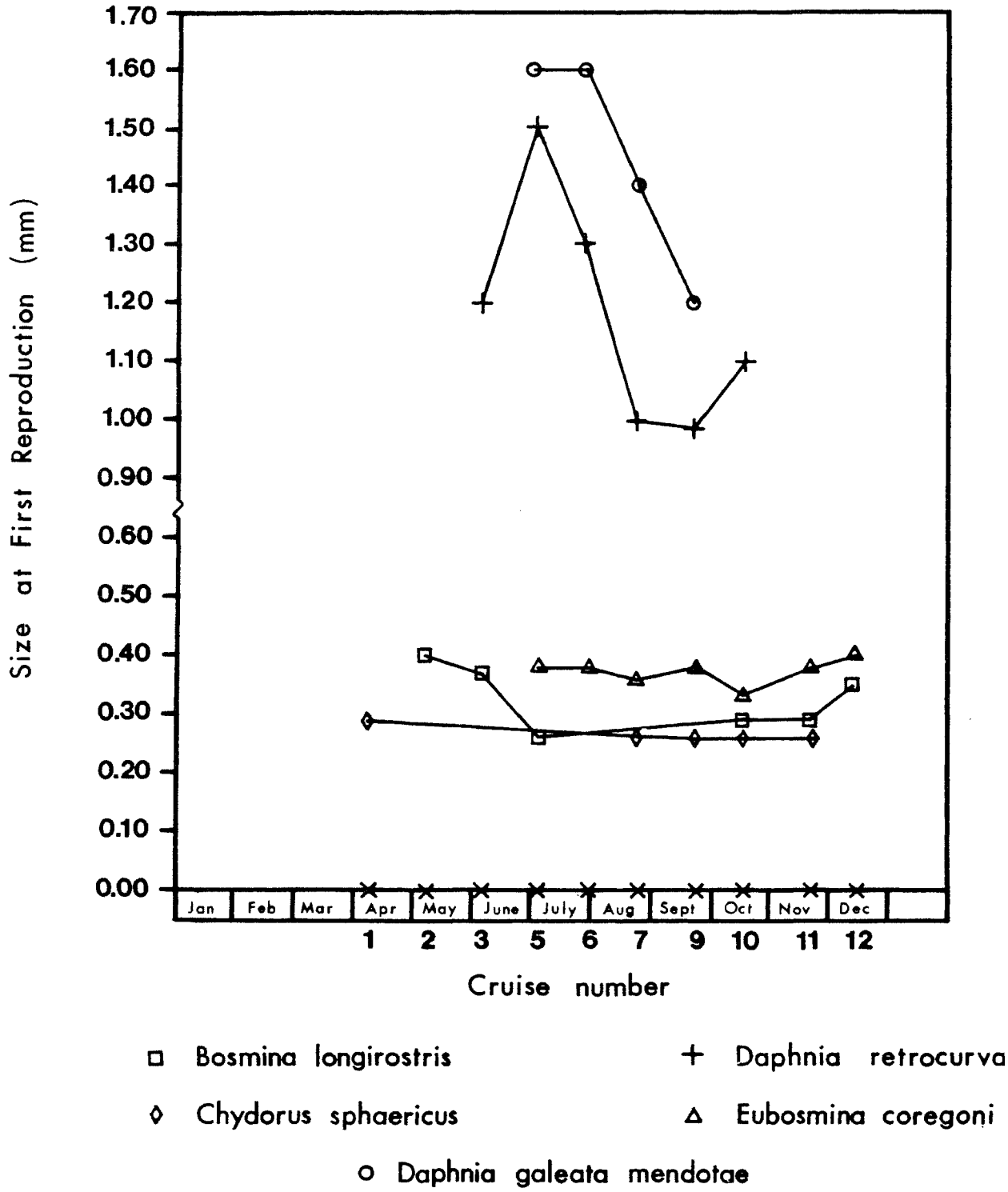

Figure 13. Size at first reproduction for major cladoceran species from thirty stations in Lake Erie, 1970.

between the two cyclopoid species (C. b. thomasi and M. edax) which are both predators as adults(Fig. 14).

PROSPECTUS

It was intended that the computer program be set up in such a fashion that studies like those described previously could be performed and so future zooplankton studies could also be used as input to the program to calculate productivity. There are several other areas which will be explored in the near future. The first of these is a size-specific production calculation. Because size-frequency measurements are integral to the production calculations of each taxon except the rotifers, it will be simple to apportion the productivity of each taxon into standard size classes, thus allowing us to compute the biomass productivity rate of given size classes of zooplankters independent of species. Predation studies are looking increasingly at the depressibility of resources, and we are particularly interested in knowing how susceptible certain size classes are to predation, for example, all individuals greater than 1 mm. Fish have been shown to be particularly selective in their predation, choosing large zooplankters preferentially, beginning at about 1 mm. We have recently shown this to be true for larval northern pike feeding on C. b. thomasi whereas previous studies have concentrated on fish such as perch, alewives, and shad which are planktivorous at much larger sizes (25 cm) than the northern pike (25 mm) in our study. The suitability of the Western Basin of Lake Erie as a nursery ground for predaceous species like the pike, walleye, sauger, etc. may depend greatly on the productivity and depressibility of specific size classes of zooplankton, independent of species composition.

There have been several other studies of zooplankton abundance in Lake

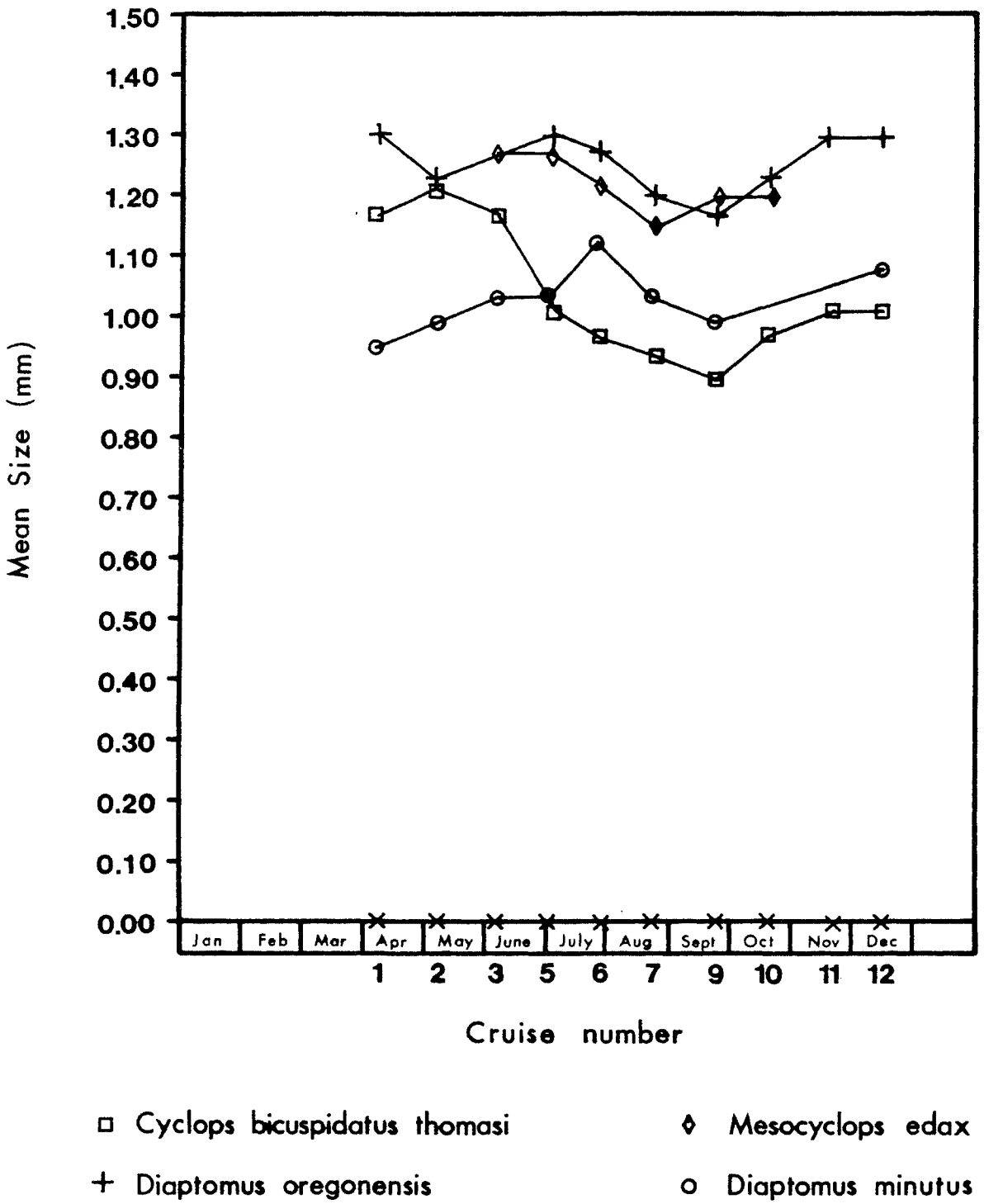

Figure 14. Mean length of copepodite 6 females from 30 stations in Lake Erie, 1970.

Erie and the other Great Lakes in recent years, and it will be interesting to run those data through this program to see how specific taxa as well as the whole community productivities change seasonally and from year to year. Recent data (Herdendorf, Personal Communication) indicate that phosphorus loading to Lake Erie has not increased during the past five years, so it will be particularly interesting to assess zooplankton productivity patterns during this period.

Finally, there has been a significant effort in recent years to assess the water quality in the nearshore areas of Lake Erie. The studies listed here for 1970 were primarily open water areas, but those stations that were nearer shore demonstrated that zooplankton productivity was higher there. An analysis of the rates of zooplankton production in the nearshore areas will enable us to better estimate the whole-lake productivity of this trophic level.

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* Publications sponsored at least in part by this research grant (OWRT-A048-OHIO).

APPENDIX I.

ZOOPLANKTON ABUNDANCE INPUT FORMATS FOR BAY OF QUINTE DATA

One card per species for a given depth, station and date

Columns 1-6 Date coded as 23 March 1975 = 750323 (Format I6)

Column 7 blank

Columns 8-10 Station code e.g. 020 for Corral 2 in Bay of Quinte, 070 for Bay (Format I3)

Column 11 blank

Columns 12-14 Species code. There is a code for the 40 spp commonly found in the Bay of Quinte corrals, but there is also a more comprehensive code of approximately 140 spp, designed to include the major Great Lakes spp. The two codes do not agree on some spp. (Format I3)

Column 15 blank

Columns 16-20 Upper depth of stratum sampled (Format F5.2)

Columns 21-25 Lower depth of stratum sampled (Format F5.2)

Column 26 blank

Column 27-30 Temperature of water °C (Format F4.1)

Columns 31-78 Abundance values 8 fields of F6.2 Units: #/liter

Order of Variables:

Copepods: Total, Total adults, eggs, nauplii, copepodites, adult females, adult males

Rotifera: Total, Total adults, eggs

Cladocera: Eggs, ovigerous, non-ovigerous, non-ovigerous plus ovigerous

For cases where presence or absence of eggs was not noted on cladocera, enter the number per liter in the non-ovigerous plus ovigerous column.

For cases when adults were not sexed in copepods, enter adults in Total adults column.

Nauplii are listed as the species bearing eggs at that time when there is no confusion, otherwise, they are listed as calanoid or cyclopoid nauplii. Unidentified copepodites have the same code as unidentified nauplii but are put in the appropriate column.

ZOOPLANKTON MEASUREMENT INPUT FORMATS

The current frequency distribution programs expect a card of the format shown on page 1, followed by any number of cards of measurements for that species, ovigerous measurements first and then non-ovigerous measurements. A set thus consists of a minimum of three cards. The final card of each group of measurements (e.g. the end of the ovigerous measurements) is signified by a 9 in column 1. Measurements are usually inputted directly as micrometer units, but may alternately be inputted as millimeters.

Column 1. card number control variable, either blank (more cards coming) or 9 (last card in set)

Columns 2-11. These columns are the sample id columns and are ignored by the current proportional frequency programs. However, each card should be uniquely identified for ease of sorting. The current id scheme is as follows:

Columns 2-4 Date code. The sampling dates were numbered from 1-25.
Column 5 blank
Column 6 Station code (as 2 = corral 2)
Column 7 blank
Columns 8-10 Species code, although only the first two digits are used.
Column 11 Depth code. 0-1 m = 1, 1-2 m = 2, 2-3 m = 3, 3-4 m = 4
Column 12 blank

Columns 13-15 Microscope Id #. We use the last three digits of the WILD number stamped on our scopes.

Column 16 blank

Columns 17-18 Magnification at which the measurements were done.

Column 19 blank

Columns 20-21 Number of measurements on this card. Maximum of 19 for micrometer unit input, maximum of 11 for millimeter input. Be sure to put in a card with a 9 in column 1 and a 1 in column 21 if one type of measurement is missing (i.e. no non-ovigerous measurements).

Column 22 blank

Column 23 Ovigerous or non-ovigerous indicator for cladocerans are 0 and 1. For copepods, 2 = Nauplii, 3 = copepodites, 4 = females, 5 = males (adults).

Columns 25-80 The actual measurements. For micrometer unit input, format = 19I3

For millimeter input, format = 11F5.4
Larger critters are measured to fewer decimal places.

APPENDIX II.

DEVELOPMENT TIME EQUATIONS USED FOR CALCULATING PRODUCTION OF GREAT LAKES ZOOPLANKTON. In several cases we fit the polynomials to the data listed in the source cited. D = development time in days, T = temperature (°C)

Species	Stage	Equation	Reference
Cyclops bicuspidatus thomasi	eggs	$D = 18932.0\ (T-4.79)^{(-1.77)}/24$	Cooley and Minns 1978
Tropocyclops prasinus mexicanus	nauplii	$D = 52.58591-6.42305T + 0.3123T^2-0.00530T^3$	Spindler 1971
	copepodids	$D = 95.23981-9.88021T + 0.40517T^2-0.00599T^3$	after Hillbricht-Ilkowska and Patalas 1967
Cyclops vernalis	eggs	$D = 3622\ (T-0.31)^{(1.45)}/24$	Cooley and Minns 1978
	nauplii	$D = 52.58591-6.42305T + 0.31213T^2-0.00530T^3$	Spindler 1971
	copedodids	$D = 95.23981-9.88021T + 0.40517T^2-0.00599T^3$	after Hillbricht-Ilkowska and Patalas 1967
Mesocyclops edax	eggs	$D = 6736\ (T + 1.69)^{(-1.50)}/24$	Cooley and Minns 1978
	nauplii	$D = 52.58591-6.42305T + 0.31213T^2-0.00530T^3$	Spindler 1971
	copepodid	$D = 95.23981-9.88021T + 0.40517T^2-0.00599T^3$	after Hillbricht-Ilkowska and Patalas 1967
Diaptomus oregonensis	eggs	$D = 53223\ (T-4.48)^{(2.11)}/24$	Cooley and Minns 1978
Diaptomus sicilis	nauplii	$D = 102.06084-13.13032T + 0.64076T^2-0.01055T^3$	Nauwerck 1963
Diaptomus siciloides	copepodid	$D = 54.24854-6.51653T + 0.32663T^2-0.00569T^3$	Nauwerck 1963
Eurytemora affinis			
Limnocalanus macrurus			
Diaptomus minutus	eggs	$D = 355133\ (T-9.6)^{(-2.52)}/24$	Cooley and Minns, 1978
Diaptomus ashlandi	nauplii	$D = 102.06084-13.13032T + 0.64076T^2-0.01055T^3$	Nauwerck 1963
	copepodid	$D = 54.24854-6.51653T + 0.32663T^2-0.00569T^3$	Nauwerck 1963
Alona affinis	eggs	$D = \text{Exp}\ [3.6144-0.2507(\ell n\ T)]^2$	Bottrell 1975
	juveniles	$D = 5(\text{Exp}\ [2.9618-0.2199(\ell n\ T)]^2)$	Bottrell 1975
Bosmina longirostris	eggs	$D = 11.96853-0.77118T + 0.01324T^2$	after Hillbricht-Ilkowska and Patalas 1967
Eubosmina coregoni	juveniles	$D = 25.68741-1.69111T + 0.03122T^2$	after Hillbricht-Ilkowska and Patalas 1967
Chydorus sphaericus	eggs	$D = 992727-0.622605T + 0.01028T^2$	after Hillbricht-Ilkowska and Patalas 1967
	juveniles	$D = 22.01189-1.13786T + 0.00534T^2 + 0.00033T^3$	after Hillbricht-Ilkowska and Patalas 1967
Daphnia galeata mendotae	eggs	$D = 13.83077-1.23375T + 0.04338T^2-0.00058T^3$	Hall 1964
Daphnia ambigua	juveniles	$D = 31.68811-2.07378T + 0.0368T^2$	Munro and White 1975
Daphnia longiremis			
Daphnia retrocurva			
Holopedium gibberum			
Ceriodaphnia lacustris			
Diaphanosoma leuchtenbergianum	eggs	$D = 13.24615-0.93187T + 0.01786T^2$	after Hillbricht-Ilkowska and Patalas 1967
	juveniles	$D = 20.60838-0.69033T-0.04551T^2 + 0.00306T^3$	after Hillbricht-Ilkowska and Patalas 1967
Leptodora kindtii	eggs	$D = 18.37356-0.87695T + 0.04947T^2-0.00289T^3+ 0.00005T^4$	
	juveniles	$D = 31.68811-2.07378T + 0.03684T^2$	Munro and White, 1975
ROTIFERS (all species)	eggs	$D = e^{(2.7547-0.2484\ \ell n\ T\ -\ 0.2408\ \ell n\ T^2)}$	Bottrell 1975

APPENDIX III.

GREAT LAKES ZOOPLANKTON SPECIES CODE LIST

COPEPODA

005 Cyclopoida

Cyclops
010 Cyclops bicuspidatus thomasi
015 Cyclops vernalis

Eucyclops
020 Eucyclops agilis
025 Eucyclops speratus

Macrocyclops
030 Macrocyclops albidus

Mesocyclops
035 Mesocyclops edax

Paracyclops
040 Paracyclops fimbriatus poppei

Tropocyclops
045 Tropocyclops prasinus mexicanus

050 Calanoida

Diaptomus
055 Diaptomus ashlandi
060 Diaptomus minutus
065 Diaptomus oregonensis
070 Diaptomus pallidus
075 Diaptomus reighardi
080 Diaptomus sicilis
085 Diaptomus siciloides

Epischura
090 Epischura lacustris

Eurytemora
095 Eurytemora affinis

Limnocalanus
100 Limnocalanus macrurus

Senecella
105 Senecella calanoides

110 Harpacticoida

Bryocamptus
115 Bryocamptus nivalis

Canthocamptus
120 Canthocamptus robertcokeri

Mesochra
125 Mesochra alaskana

Moraria
130 Moraria cristata

CLADOCERA

135 Alona sp.
140 Alona affinis
145 Alona guttata
150 Alona intermedia
155 Alona quadrangularis

Bosmina
160 Bosmina longirostris

Camptocercus
165 Camptocercus rectirostris

Ceriodaphnia
170 Ceriodaphnia lacustris
175 Ceriodaphnia quadrangula

Chydorus
180 Chydorus sphaericus

Daphnia
185 Daphnia ambigua
190 Daphnia galeata mendotae
195 Daphnia longiremis
200 Daphnia longispina
205 Daphnia parvula
210 Daphnia pulex
215 Daphnia pulicaria
220 Daphnia retrocurva

Diaphanosoma
225 Diaphanosoma brachyurum
230 Diaphanosoma leuchtenbergianum

Eubosmina
235 Eubosmina coregoni

Eurycercus
240 Eurycercus lamellatus

Holopedium
245 Holopedium gibberum

Illyocryptus
250 Illyocryptus sordidus

Latona
255 Latona setifera

Leptodora
260 Leptodora kindtii

Leydigia
265 Leydigia acanthocercoides
270 Leydigia quadrangularis

Moina
275 Moina brachiata

Pleuroxus
280 Pleuroxus procurvus

Polyphemus
285 Polyphemus pediculus

Sida
290 Sida crystallina

295 Malacostraca

Mysis
300 Mysis relicta

ROTIFERA
301 Anuraeopsis fissa

305 Asplanchna sp.
307 Asplanchna brightwelli
310 Asplanchna girodi
315 Asplanchna herricki
320 Asplanchna priodonta

325 Brachionus sp.
330 Brachionus angularis
335 Brachionus budapestiensis
340 Brachionus calyciflorus
345 Brachionus caudatus
350 Brachionus diversicornus
355 Brachionus havanaensis
360 Brachionus patulus
365 Brachionus quadridentatus
367 Brachionus rubens
370 Brachionus urceolaris
375 Chromogaster sp.
380 Chromogaster ovalis

385 Cephalodella sp.

390 Collotheca sp.
395 Collotheca mutabilis
400 Collotheca pellagica

405 Conochiloides sp.
410 Conochiloides dossuarius
415 Conochiloides exiguus

420 Conochilis sp.
425 Conochilis unicornus

430 Epiphanes sp.
431 Epiphanes clavulata
435 Epiphanes macroura
437 Epiphanes pelagica

440 Euchlanis sp.
445 Euchlanis dilatata
447 Euchlanis triquetra

450 Filinia sp.
455 Filinia longiseta
460 Filinia terminalis

465 Gastropus sp.
467 Gastropus hyptopus
470 Gastropus stylifer

475 Hexarthra sp.
480 Hexarthra mira

485 Kellicottia sp.
490 Kellicottia bostoniensis
495 Kellicottia longispina

500 Keratella sp.
505 Keratella cochlearis
510 Keratella crassa
515 Keratella earlinae
520 Keratella hiemalis
525 Keratella hispida
530 Keratella quadrata
535 Keratella taurocephala

540 Lecane sp.
545 Lecane luna
547 Lecane flexilis
548 Lophocharis salpina
550 Monostyla sp.
555 Monostyla bulla
556 Monostyla closterocerca
557 Monostyla lunaris
560 Notholca sp.
565 Notholca acuminata
570 Notholca foliacea
572 Notholca laurentiae
575 Notholca squamula
580 Notholca striata

585 Platyias sp.
590 Platyias patulus
592 Platyias quadricornis

595 Ploesoma sp.
600 Ploesoma hudsonii
605 Ploesoma lenticulare
610 Ploesoma truncatum

615 Polyarthra sp.
620 Polyarthra dolichoptera

625 Polyarthra euryptera
630 Polyarthra longiremis
635 Polyarthra major
640 Polyarthra remata
645 Polyarthra vulgaris

650 Pompholyx sp.
655 Pompholyx sulcata

660 Rotaria sp.

665 Squatinella sp.

670 Synchaeta sp.
671 Synchaeta asymmetrica
672 Synchaeta grandis
673 Synchaeta kitina
674 Synchaeta lakowitziana
675 Synchaeta pectinata
680 Synchaeta stylata

685 Trichocerca sp.
690 Trichocerca cylindrica
695 Trichocerca longiseta
700 Trichocerca multicrinis
701 Trichocerca porcellus
702 Trichocerca pusilla
703 Trichocerca rousseleti
705 Trichocerca similis

710 Trichotria sp.
715 Trichotria tetractis
720 Rotifer (unid)

725 eggs